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Ecology of Band-tailed Pigeons in Oregon



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Cover illustration: A flight of band-tailed pigeons (Columba Fasciata) in Oregon's Coast Range mountains.

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By

Robert L. Jarvis and Michael F. Passmore

United States Department of the Interior
Fish and Wildlife Service
Washington, D.C. 20240

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Ecology of Band-tailed Pigeons in Oregon

by

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Abstract. The ecology of band-tailed pigeons (*Columba fasciata*) was investigated in western Oregon to assess the roles of survival and recruitment to population status and the relation of food, minerals, and diet to reproduction strategy. Band-tailed pigeons congregated at mineral deposits to consume minerals from mid-June to mid-September. Males generally arrived and departed between daylight and 1000 h and females between 0930 and 1200 h, the inverse of the nest attentive schedules for the sexes. The pigeons used one or several adjacent mineral sites throughout the summer and most returned to the same mineral site in subsequent years. Band-tailed pigeons were resident from April through September; migration apparently did not begin before late September. Three indirect sources of evidence indicated that fledging began in June, reached a peak in mid-August, and continued until late September. Second year (SY) band-tailed pigeons apparently began nesting later than and were about one-third as productive as adults. In Oregon, most of the adult population could fledge as many as two young over the 100–110-day nesting period, resulting in a maximum potential recruitment of 47–50% juveniles. We estimated that the fall population contained about 23% juveniles, 12% yearlings, and 65% adults. Mean annual survival of adults was 63.7%, but was year-specific. To maintain a stable population with the estimated survival rates required production near the biotic potential (40.8%). Conversely, a stable population could be attained with the estimated rate of recruitment (23%) and high but realistic rates of survival (adults, 83%; juveniles, 68%). Counts of band-tailed pigeons at mineral sites in Oregon indicated that the population had undergone two periods of modest increase (2.4–7.1% per year) and two periods of sharp decline (10.4–11.1% per year). In 1988 the population index was only 34% of the 1950–88 average.

Harvest of band-tailed pigeons in the three Pacific Coast states averaged 414,000 from 1957 to 1983; about 55% of the harvest took place in California, 23% in Washington, and 22% in Oregon. In Oregon, about 65% of the harvest took place in the first 10 days of September and 40% was at mineral sites. Fewer juveniles were shot at mineral sites (13%) than at feeding areas (25%). Hunting at mineral sites was directed at experienced breeders and may be particularly detrimental to the population. However, the overall effect of hunting on abundance was not determined.

Band-tailed pigeons fed extensively on elder (*Sambucus* spp.) and cascara buckthorn (*Rhamnus purshiana*) berries while nesting. The emergence of Pacific red elder (*S. callicarpa*) berries in June provided the food resources necessary for initiation of reproduction in Oregon, and probably throughout the Northwest. Elder berries contain little calcium (0.06–0.12%), therefore, the pigeons in the Northwest may require a mineral supplement in their diet. Mineral sites may be the scarcest resource required for reproduction by band-tailed pigeons in the Northwest.

Key words: Band-tailed pigeons (*Columba fasciata*), diet, mineral sites, Oregon, Pacific Northwest, population trend, recruitment, survival.

The Columbidae is a large, diverse group of birds that is mostly tropical in distribution; few species are seen at North Temperate latitudes (Goodwin 1970). The native ranges of only three species of columbids include

the North Temperate portions of North America: the extinct passenger pigeon (*Ectopistes migratorius*), the mourning dove (*Zenaidura macroura*), and the band-tailed pigeon (*Columba fasciata*). Although passenger pigeons were, and mourning doves are, numerous and widely distributed, band-tailed pigeons are restricted to coniferous forest zones in mountainous areas of western North America.

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The band-tailed pigeon of temperate North America has close taxonomic links to New World tropical pigeons. Along with the Jamaican band-tailed pigeon (*C. caribaea*) and the Chilean pigeon (*C. araucana*), *C. fasciata* forms a superspecies (Goodwin 1970). The range of *C. fasciata* extends through Central America into mid-South America. Eight races of the species are recognized; only two exist in North America north of Mexico (American Ornithologists Union 1957). In North America, *C. f. fasciata* is present in the southern Rocky Mountains (Colorado, Utah, New Mexico, Arizona, West Texas, and Mexico) and *C. f. monilis* along the Pacific Coast (southern Alaska to northern Baja California, Fig. 1A). It is this latter race we examine in this monograph.

Like all columbids, band-tailed pigeons have well-known and unique life history traits. Single egg clutches and sequential attempts at nesting are normal (Grinnell 1913; Fitzhugh 1970), although two egg clutches have been reported (Neff 1947; MacGregor and Smith 1955). Both adults incubate clutches and feed the young crop milk on a fixed schedule: males attend nests from mid-morning until midafternoon and females from midafternoon until the following midmorning (Neff 1947; MacGregor and Smith 1955; Peeters 1962; Zeigler 1971). Successive attempts at nesting take place at 45–50 day intervals (18 days of incubation, 22–24 days of brooding, and up to 7–8 days of respite; Zeigler 1971). Females seemingly sometimes lay and begin incubating the egg for the next nest before the previous young is fledged,

thereby accelerating the nesting cycle (Fitzhugh 1970). Nesting seasons are not well defined, especially in the southern portion of the range, and timing of nesting is clearly dependent upon availability of food (Gutiérrez et al. 1975); photoperiod seems to play only a minor role in timing of reproduction events. Unseasonable nesting—fall and winter—when food is abundant has been reported in California, New Mexico, and Arizona (Stephens 1913; Allen 1941; Neff 1947; MacGregor and Smith 1955; Gutiérrez et al. 1975).

Migration seems to be a variable trait in band-tailed pigeons. Birds in the southern portion of their range are non-migratory or weakly migratory and have been described as nomadic (Neff 1947; Smith 1968). In contrast, birds in the northern portion of their range are strongly migratory with predictable arrival and departure times: birds arrive in March through May and depart in September (Grinnell 1913; Neff 1947; Smith 1968). Probably as a consequence of regular migratory schedules, the reproduction season in the north is regular and predictable: May through August (Neff 1947; Glover 1953). Statements about migration and reproduction schedules in the northern portion of the range must be tempered because neither are based on firm, quantified data. Migration schedules are based on casual observations of flocks of pigeons rather than on regular counts. Reproduction schedules are based on a few incidental observations of nests; no studies have been published on nesting of the band-tailed pigeon in the northern portion of its range.

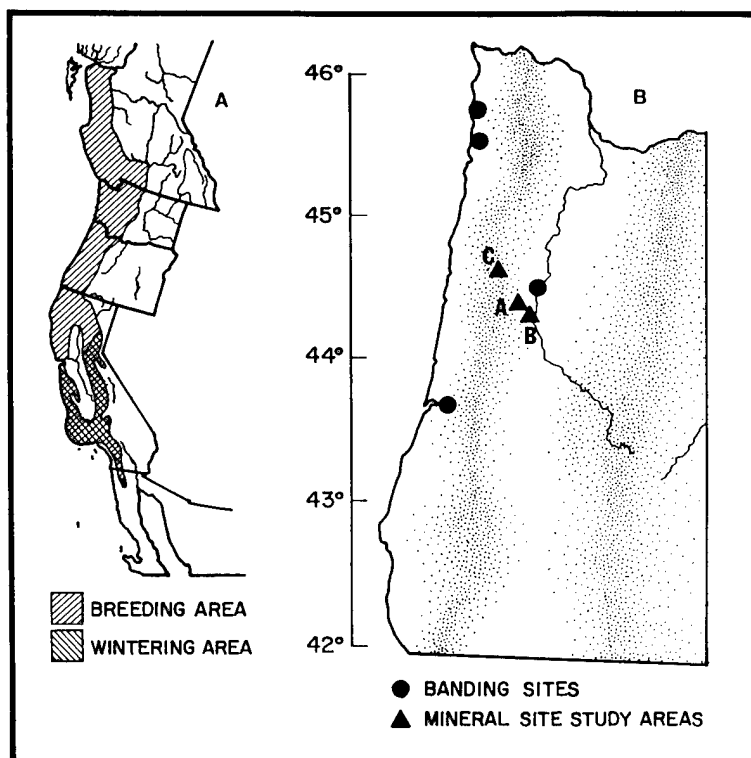


Fig. 1. A) Distribution of band-tailed pigeons along the Pacific Coast of North America (Jeffrey et al. 1977). B) Location of banding and mineral site study areas in western Oregon.

Regular, consistent use of mineral sites by band-tailed pigeons is a characteristic observed in the Pacific Northwest. Originally, mineral consumption was thought to be a phenomenon related to fall migration (Morse 1957), but recent work indicates it is associated with reproduction during the summer (March and Sadleir 1972). March and Sadleir (1975) speculated that calcium, needed for production of eggs and crop milk, was the essential item sought by pigeons at mineral sites. Concentration of band-tailed pigeons at mineral sites has occasionally been reported in other parts of their range, but mineral use is less common (Smith 1968; Fitzhugh 1970).

Band-tailed pigeons were hunted for both sport and market during spring and winter in the decades before and just after 1900 (Neff 1947). During winter 1911–12 a concentration of pigeons in California resulted in a large harvest which prompted the closing of hunting season beginning in 1913. Complaints of crop depredation resulted in reopening of sport hunting seasons in the Pacific states in 1932. Hunting seasons have continued until the present. Annual collection of data by state conservation agencies was initiated in the 1950's on the number of pigeons harvested and the number of hunters (Jeffrey et al. 1977). Attempts to develop indexes to abundance of pigeons were mostly unsuccessful.

With the development of the Accelerated Research Program of the U.S. Fish and Wildlife Service in 1967, interest in band-tailed pigeons was stimulated. Two early results of that interest were a review of the published literature (Fitzhugh 1970) and a review of hunting and population data gathered by state conservation agencies (Jeffrey et al. 1977). The latter authors recommended coordinated research programs to develop an enlarged knowledge base for management of band-tailed pigeons. The first such effort took place in the southern Rocky Mountain states and the results of that program were extensively reported (Fitzhugh 1970; Braun 1972; 1976; Braun et al. 1975; Gutiérrez et al. 1975; Kautz and Braun 1981; White and Braun 1978, 1990; Curtis and Braun 1983; Curtis et al. 1983). A second research effort in the Pacific states took place in the mid-1970's, but the results have not been widely distributed (McCaughan and Jeffrey 1980; Slosson and Goss 1982). Further, little effort has been made to integrate results of specific research projects to provide a better overall understanding of the ecology of band-tailed pigeons. We seek to partially remedy that situation by presenting our results from Oregon and by integrating them with other sources of information to develop a conceptual model of the population biology of band-tailed pigeons. Specifically, we examined the relations between food, nesting chronology, mineral consumption, and recruitment, and we integrate these relations with survival, population trends, and hunting.

We are indebted to many people for information and data. Unfortunately, the long time span over which

some data sets were generated prevents us from identifying all individuals who contributed to this report. Nonetheless, we acknowledge those who worked anonymously and hope they will recognize the fruits of their labors.

Counts of band-tailed pigeons at mineral sites from 1950 to 1988 were made by biologists of the Oregon Department of Fish and Wildlife (ODFW). During the 1950's and 1960's the pigeons were banded by W. M. Batterson (ODFW) and by U.S. Fish and Wildlife Service Game Management Agents. Many Oregon State University students assisted in banding pigeons in the 1960's and 1970's.

The late H. M. Wight and his graduate students laid much of the foundation upon which our work is based (Wight et al. 1967; Silovsky et al. 1968; Silovsky 1969; Sisson 1968; Zeigler 1971); they also banded pigeons in the late 1960's and made their reports and notes available to us. C. E. Kebbe (ODFW), H. T. Harper (California Fish and Game [CFG]), and R. G. Jeffrey (Washington Department of Game [WDG]) were instrumental in initiation of our studies of band-tailed pigeons. They, along with R. D. Goss (CFG), R. R. Denny (ODFW), and C. F. Martinson (WDG), provided information from their studies and surveys, and freely exchanged ideas and suggestions about band-tailed pigeons.

Our studies were funded by the Accelerated Research Program of the U.S. Fish and Wildlife Service. The section on mineral site use was based on an M.S. thesis by M. F. Passmore. Drafts of this report were reviewed by B. J. Verts, R. E. Tomlinson, C. E. Braun, J. E. Kautz and an anonymous reviewer.

Study Area

Our study area encompassed all of Oregon west of the Cascade Mountains (Fig. 1B). Survey data on pigeon populations and hunters were collected throughout this region, but most data were from the Willamette Valley and the Coast Range Mountains.

Western Oregon is characterized by dense coniferous forests in mountainous regions (temperate rain forests) and diversified agriculture in the Willamette Valley (Highsmith and Kimerling 1979). Most forested areas are managed for timber production with Douglas fir (*Pseudotsuga menziesii*), the predominant commercial species. Clear-cutting is the usual method of harvest, therefore forests are a patchwork of different but even-aged stands. Brush, many species of which are prolific berry producers, invades rapidly after clear-cutting unless eliminated through intensive management. Agricultural crops in the Willamette Valley include fruit and nut orchards, row crops (beans, sweet corn, carrots), wheat, and ryegrass. In coastal valleys, dairy farming is the principal agricultural activity. Winters are wet and mild;

annual rainfall ranges from 100 to 400 cm and temperatures are rarely below freezing for extended periods. Summers are warm and dry but short (2.5–3 months). Along the coast, fog or strong winds are common during summer. Elevations in the Willamette Valley are about 75 m. Maximum elevation in the Coast Range is about 1,500 m and most of the Coast Range is steep with well-defined drainages.

Intensive studies were conducted at three specific mineral sites within the study area, two on the western edge (Sites A and B, Fig. 1B) of the Willamette Valley and a third in the Coast Range (Site C). The three sites were an abandoned artesian salt well, a water collection basin, and a gravel bar along a small stream that contained a salt deposit exposed during construction of a levee. The mineral sites had deciduous and coniferous trees nearby that were used as perches by pigeons both before and after consuming mineral. All sites were within 40 km of Corvallis (Passmore 1977).

Methods

Data analyzed in this report came from a variety of sources: banding by us and others, surveys by the ODFW, mail questionnaires and parts (wing) collections, collection of pigeons, and intensive observation of pigeons at mineral sites.

Trapping was with cannon and rocket nets over sites baited with wheat, cracked corn, and occasionally other grains. Some pigeons were trapped where they congregated at mineral sites, but because pigeons used mineral sites primarily during summer, few opportunities for trapping at these sites occurred in spring.

Data were also used from pigeons banded during spring (April–June) at several locations in western Oregon from 1950 to 1979. For pigeons banded by us (1975–78) at Corvallis, classification of age and sex was based on plumage and cloacal characters (Miller and Wagner 1955; Houston 1963; Silovsky et al. 1968; White and Braun 1978). Age was classified as juvenile (calendar year of hatching), SY (1st calendar year after hatching), and after second year (ASY, 1+ years old). SY birds were identified by the presence of remnant juvenal secondary coverts and unmolted juvenal primaries VIII, IX or X (White 1973). Age structure of the population was estimated from samples where each bird was assigned to one of the three age classes. Other banders usually did not designate sex and classified age as juvenile or after hatching year (AHY). Survival rates were calculated with the Seber–Robson–Youngs model (Model I; Brownie et al. 1978) only for adults banded in spring. This model assumed survival and recovery rates were age-independent but year specific (Seber 1970; Robson and Youngs 1971). Survival rates for juveniles could not be calculated because too few were banded.

Pigeons were collected by shooting from April through September in 1976 and 1977; collections were made twice a week throughout that period. All collections were within 80 km of Corvallis. We searched extensively for pigeons, and collected birds wherever possible, but most were taken at feeding areas, mineral sites, flyways to and from mineral sites and feeding areas, and incidentally wherever birds were observed. Data recorded for each pigeon collected included age, sex, time of day, and activity. The crop and gizzard were removed and contents examined for food and grit. Food items in the crop and gizzard were identified by comparison with materials in a reference collection. Crop glands were examined and classed as active (producing crop milk), developing, regressing, or undeveloped (Zeigler 1971).

We used several indirect methods to estimate nesting phenology because band-tailed pigeons nested in dense forest vegetation in mountainous terrain (Neff 1947; Glover 1953; MacGregor and Smith 1955) and the likelihood of finding enough nests to document nesting ecology was slight. The four indirect methods used were

1. crop gland activity of band-tailed pigeons collected in 1976–77,
2. distribution of specific reproduction events (e.g., egg in oviduct) from collected birds,
3. seasonal appearance of juveniles at mineral sites, and
4. age distribution of juveniles shot by hunters.

To generate a fledging curve from the temporal distribution of crop gland activity, we made several assumptions based on Zeigler (1971). We assumed the crop gland was undeveloped during the 1st week of incubation, developed during the 2nd week, was active from the 3rd week (band-tailed pigeons have an 18-day incubation period) through the 6th week of the cycle (3rd week of brooding), and regressed during the 7th week of the cycle. Further, fledging took place at the beginning of the 7th week (day 42) and the egg of the next nesting cycle was laid at the beginning of the 8th week (day 51 of the previous cycle).

We combined samples from both years, grouped specimens into 2-week periods based on date of collection, and assigned each specimen to one of seven categories based on stage of activity of the crop gland. These were undeveloped, developing, regressing, and active (four categories).

Each category corresponded to 1 week of the 7-week nesting cycle. However, the crop gland was active for 4 weeks of the cycle but the exact stage of an active crop gland could not be determined by visual inspection of the gland. We assumed that pigeons with active crop glands were uniformly distributed among the 4 weeks during which the gland was active. Thus, for each 2-week collection period, we assigned 25% of the pigeons with active crop glands to each of the four active categories.

Each category corresponded to the week in which young would fledge according to the following schedule:

regressing, week of collection; active IV, 1 week after collection; active III, 2 weeks after collection; active II, 3 weeks after collection; active I, 4 weeks after collection; developing, 5 weeks after collection. Birds having undeveloped crop glands were not used to estimate fledging dates because it was not known if they were in a nesting cycle. Because sample sizes varied, data were entered as the proportion of the number collected during each 2-week period. The result was a three-dimension matrix with week of collection on one axis, week of fledging on another, and crop gland stage on the third. Summation of the matrix by week of fledging (across week of collection and crop gland stage axes) generated a fledging curve.

In the second method of generating a fledging curve from band-tailed pigeons collected in 1976–77, specimens were examined for a specific event in the reproduction cycle. The evidence and events they represented were regressing crop gland, young fledged 5 days before date of collection; developing crop gland, egg laid 10 days before date of collection; egg in oviduct, egg laid 1 day after collection. Estimated fledging dates were plotted as a frequency distribution.

Juvenile band-tailed pigeons visited mineral sites and we used their appearance to examine reproduction phenology. During observations at mineral sites, numbers of adults (including yearlings) and juveniles were recorded every 15 min. Daily average percent of juveniles was calculated from these counts.

From 1974 to 1976 we conducted intensive studies of pigeons at three mineral sites (Passmore 1977). These studies were designed to identify daily and seasonal patterns of appearance at mineral sites of the different age and sex classes of pigeons. Pigeons were captured at mineral sites with rocket nets as they consumed minerals, and a patagial wing tag (3 × 11 cm) was attached to each wing. During the 3 years, 748 pigeons was tagged; 257 in 1974, 428 in 1975, and 63 in 1976. In 1974 tags were attached with a nylon fastener, and whereas retention of tags was satisfactory during summer 1974, retention until summer 1975 was modest. Consequently, in 1975 and 1976 stainless steel pins were used and tag retention between 1975 and 1976 improved. Recaptured pigeons that had lost one or both tags were retagged. By 1976 many tagged birds were present, and to minimize disturbance from trapping we only trapped five times at two mineral sites (sites B and C).

Observations of pigeons at the three mineral sites were conducted daily from daylight until 1200 h beginning on 23 June in 1975 and on 16 June in 1976. Nearly all pigeons that visited mineral sites arrived in the morning and departed by 1200 h; few pigeons appeared at mineral sites before mid-June (Passmore 1977). In 1974, observations were made at about 3-day intervals beginning on 7 July. In all years, observations continued until 31 August at sites B and C, where hunting commenced

on 1 September, but continued into September at site A.

A daily log was maintained at each mineral site of

1. arrival and departure of pigeons;
2. initial and repeat sighting of tagged birds by identification code;
3. consumption of mineral; and
4. behavioral activities such as courtship, feeding, sunning or bathing, and response to predators.

At 30-min intervals throughout the observation period we recorded temperature, wind velocity, cloud cover, number of pigeons present, identity of tagged individuals, and number of pigeons engaged in different behaviors (preening, resting, courting, etc.). Age was determined by the presence (adult) or absence (juvenile) of the white nape stripe; only pigeons with the nape clearly exposed to the observer were counted. All observations were made with 7–10× binoculars and 20–80× spotting scopes.

Daily observation rates of tagged band-tailed pigeons at mineral sites was determined as:

$$R = N_i / X_i,$$

where

- R = daily rate of observation of tagged band-tailed pigeons,
- N_i = number of observations of pigeon i , and
- X_i = number of opportunities for pigeon i to be observed (number of days of observations between tagging and 31 August).

Observation rates were calculated only for band-tailed pigeons observed at least once after tagging and were calculated separately for adults and juveniles at each site.

Homing rates of band-tailed pigeons in subsequent years to the original site at which they were tagged were calculated by:

$$F_{ijx} = (R_{ijx} C_{ij}) / (N_{ix} S_{ij}),$$

where

- S_{ij} = estimated survival rate from year i to year j ,
- R_{ijx} = number of tagged birds observed in both year i and year j at site x ,
- N_{ix} = number of tagged birds observed in year i at site x , and
- C_{ij} = correction for loss of tags between year i and year j .

The correction factor for lost tags was estimated from the number of birds observed with one tag and with

two tags, using a binomial probability function (Seber 1973). The procedure requires that tags on the right and left wings had an equal and independent probability of being lost, a likely assumption because tags were attached in an identical manner. We also assumed that birds with one tag were seen at the same rate as those with two tags, an assumption that was probably not true. However, in 1975 and 1976, observations were made continuously from daylight until 1200 h at all three sites from mid-June until 31 August; individual pigeons remained at the sites for 1–2 h and identification of tagged birds was the highest priority data gathered. Thus, we believe that violation of the assumption of equal observation rates of birds with one and two tags was minimal. We did not use data from band-tailed pigeons that were recaptured only, because we were attempting to capture unmarked birds, a procedure that would produce a biased sample of birds that had lost none, one, or two tags.

Data on harvest and population abundance were derived from two surveys conducted annually by the ODFW. The harvest survey consisted of a mail questionnaire sent to a random sample of 10% of those who purchased an Oregon hunting license. This questionnaire requested harvest information on all species that could be hunted legally and was mailed following the close of the last hunting season (usually in January). Undoubtedly some bias occurred because of the long interval from the pigeon hunting season (September) and the mailing of questionnaires (January–February) and because of the number of species for which information was requested. However, the procedure for collecting these data was consistent over the relevant time span. Therefore, the estimated harvest provided an index to actual harvest, though the actual estimate possibly was biased.

Beginning in 1950, personnel of the ODFW annually counted band-tailed pigeons at some mineral sites. A biologist arrived at a site at daylight and recorded all birds arriving from then until 1200 h. These counts were made the last week of August, just before hunting season opened on 1 September. Observers attempted to count pigeons at each site once a year, but because of rain and fog, pigeons at some sites were not counted every year. Mineral sites on the coast were underrepresented because of the prevalence of fog. Fog and rain reduced visibility and rain reduced the number of pigeons visiting mineral sites (Passmore 1977), therefore, continuous records were present for only eight sites.

We developed a composite index from the counts at mineral sites by treating each site as an independent estimator of population abundance. First, the long-term mean of the number of band-tailed pigeons counted was calculated for each site and annual counts converted to proportions of those means; calculations were made independently for each site. An annual mean index then was calculated from these proportions by summing

over sites and dividing by the number of sites counted during that year.

In matrix terminology:

$$PI_i = \sum_{j=1}^8 (x_{ij} / \bar{x}_j) / n_i,$$

where

- PI_i = population index in year i ,
- x_{ij} = number of pigeons counted in year i at site j ,
- \bar{x}_j = mean number of pigeons counted at site j , and
- n_i = number of sites counted in year i .

From 1973 to 1976 we conducted a mail survey in which we requested hunters to send us wings of pigeons they bagged. This survey was identical to that conducted by Silovsky (1969). To generate a pool of pigeon hunters, we obtained a list of those hunters who indicated they bagged pigeons on the ODFW harvest survey of the previous year (initially 1972). The names of those individuals who responded positively to our survey were retained on our mailing list from one year to the next. Each hunter was mailed eight self-addressed postage paid return envelopes and instructed to place one wing from each pigeon harvested on a hunt in one envelope and mail it to us. Thus, each envelope represented one day's hunt by one hunter. We also requested information on location of hunt, date, number of birds crippled (downed and not retrieved), and type of area hunted (mineral site, flyway, feeding area, or other).

Age of wings was classified as HY, SY or ASY by the condition of secondary coverts and molt sequence and condition of primaries (White 1973). Fledging dates of juveniles were estimated by the sequence of primary feather molt (White and Braun 1978).

Results

Mineral Sites

Of 748 band-tailed pigeons trapped and tagged at three mineral sites from 1974 to 1976, 343 were observed 1,945 times. We drew most of our conclusions from continuous observations in 1975–76 when 296 tagged pigeons were observed 1,782 times during 493 observation-days (one or more observers at one site = 1 observation-day).

Seasonal Pattern of Appearance of Adults

Occasional observations revealed fewer than 10 pigeons per day visited mineral sites before mid-June. Numbers present at each site increased from about 15 per

day in mid-June when we began intensive observations to about 60 per day in mid-August (Fig. 2). Differences in seasonal occurrence of band-tailed pigeons among sites and between years are discussed by Passmore (1977) and will be only summarized here. More pigeons were observed daily at two of the three sites in 1976 than in 1975 and the pattern of increase from early to late summer was more apparent in 1976 than in 1975. Inclement weather, especially rain, was more common in 1975 than 1976 and possibly accounted for differences in numbers observed in the 2 years; rain greatly decreased the number of band-tailed pigeons visiting mineral sites (Passmore 1977). Peak numbers of adults observed at mineral sites occurred 1–2 weeks later in 1976 than in 1975, indicating slight differences in chronology of activities of band-tailed pigeons between the 2 years; response of the pigeons to weather also possibly influenced differences in chronology of use of mineral sites.

In both years the number of adults increased continuously and often dramatically from mid-June until mid- to late August at sites A and C. At site A, where pigeons were not hunted, numbers visiting the site daily decreased during September. At site B, numbers of adults visiting the site daily reached a peak in early July and declined gradually until a secondary peak was recorded in mid-August. However, the second peak was minor compared with the number of band-tailed pigeons at sites A and C during late August. Rather, the pattern of daily numbers of adult pigeons at site B was one of a modest peak in early summer with a nearly continuous decline until late August when only about 25 band-tailed pigeons continued to visit the site daily.

Daily Patterns of Appearance of Adults

Two daily periods of arrival of band-tailed pigeons

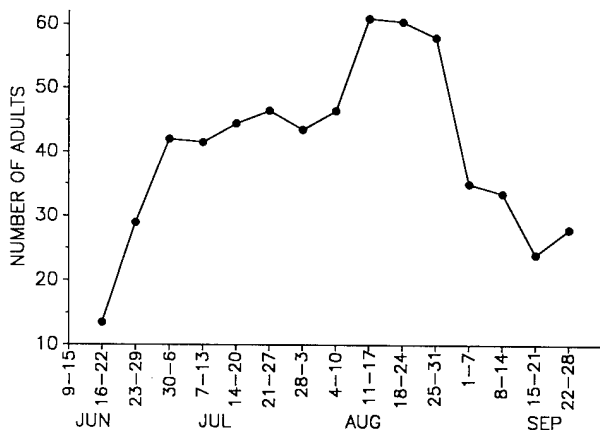


Fig. 2. Average number of adult band-tailed pigeons counted per day at three mineral sites in western Oregon, 1975–76. Data were averaged over the three sites and 2 years by biweekly periods.

at mineral sites were apparent—one in early morning (daylight to 1000 h) and one in late morning (1000–1200 h; Fig. 3). Males predominated in early morning and females in late morning (Table 1). Males usually began arriving shortly after daylight and most departed between 0900 and 0930 h; females arrived between 0930 and 1030 h and most departed by 1200 h. This general pattern probably reflected nesting responsibilities of the sexes; females attended nests until mid-morning and males attended nests from mid-morning until mid-afternoon (MacGregor and Smith 1955; Peeters 1962; Zeigler 1971).

Sex ratios of adult band-tailed pigeons visiting mineral sites were nearly even until September when a shift toward a preponderance of males was evident (Table 2). At site A, males greatly outnumbered females in September. The increased proportion of males in September coincided with the decreased number of adults visiting the mineral sites.

The proportion of males in late morning and of

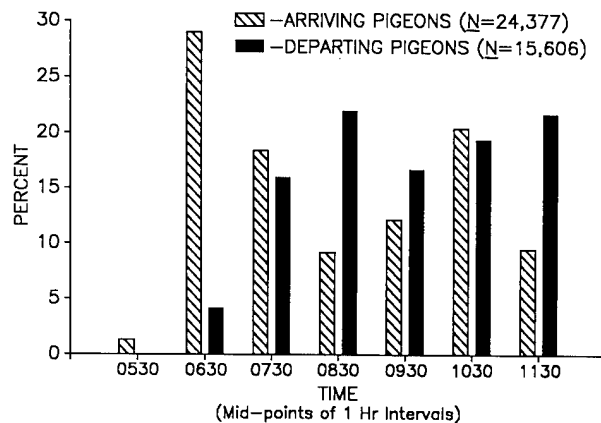


Fig. 3. Frequency distribution, by hourly periods, of band-tailed pigeons arriving and departing at three mineral sites in western Oregon, 1974–76. Arriving and departing bandtails were counted at all three sites on the same days except when trapping prevented the counting of departing birds.

Table 1. Sex of band-tailed pigeons trapped, and tagged pigeons observed, in the early morning (<0900 h) and late morning (>1000 h) at three mineral sites in western Oregon, 1975–76.

Sex	Percent of trapped pigeons		Percent of observed pigeons	
	<0900 h (N = 250)	>1000 h (N = 224)	<0900 h	>1000 h
Male	89.6	18.3	86.4	31.1
Female	10.4	81.7	13.6	68.9
Totals	100.0	100.0	100.0	100.0

Table 2. Sex ratios of tagged band-tailed pigeons observed between 0500 h and 1200 h at three mineral sites in western Oregon from 16 June to 28 September 1976.

Location	Females: male			
	June	July	August	September
Site A	1.5:1	0.9:1	0.7:1	0.2:1
Site B	0.3:1	1.3:1	1.1:1	
Site C	0.7:1	1.2:1	0.9:1	
Mean	1.0:1	1.1:1	0.9:1	0.2:1

females in early morning increased (males, $\chi^2 = 15.3$, $df = 3$, $P < 0.05$; females, $\chi^2 = 9.5$, $df = 3$; $P < 0.05$) at the end of August (Table 3). Because these were nest-attentive periods for the respective sexes, their appearance at mineral sites during those periods indicated they were not engaged in nesting. However, young are capable of thermoregulation when 9 days old (Zeigler 1971) and some adults are not continuously attentive at nests with older young (Neff 1947). At sites A and B males were abundant during late morning in late August. No females were observed at site B after 24 August. At site C, males did not increase in proportion during late morning in late August but the number of pigeons visiting site C remained high (1975) or continued to increase (1976). The proportion of females present during early morning changed little throughout the summer at site C. Thus, the increased proportion of males at mineral sites in late August and September resulted from termination of visits by females during late morning.

Activities of Band-tailed Pigeons at Mineral Sites

Although minerals seemingly were the principal attractant to band-tailed pigeons, relatively little time was spent consuming minerals (Table 4). Based on observations of tagged birds, band-tailed pigeons remained at mineral sites about 1–2 h. The pigeons spent much of

their time loafing and preening while perched in trees adjacent to the mineral deposits. Consumption of mineral took place when groups of band-tailed pigeons descended to the mineral deposit and pecked at the soil, or drank water when it was present; birds remained on the ground only briefly ($\bar{x} = 45$ sec, $N = 1,890$). Often, the pigeons made repeated excursions over the mineral deposit before landing. The slightest disturbance caused the flock to return to the trees; the cause of some disturbances seemed to be imaginary.

Hawks were commonly observed at mineral sites we studied. Immature Cooper's hawks (*Accipiter cooperii*) often attempted to capture band-tailed pigeons. While perched in trees, the pigeons seemed unconcerned with these capture attempts until a hawk closely approached (~5–10 m). However, when on the ground, the pigeons took flight at the first appearance of a hawk: even soaring red-tailed hawks (*Buteo jamaicensis*), turkey vultures (*Cathartes aura*), and coursing northern harriers (*Circus cyaneus*) caused the pigeons to abandon the mineral deposit and return to adjacent trees. These differing reactions to hawks probably reflected the arboreal habits of band-tailed pigeons and their escape mechanisms. From trees, band-tailed pigeons took flight in a steep dive and were able to escape pursuing hawks. From the ground their flight was, in comparison, slow and labored.

Courtship activities occasionally were observed and consisted of pair formation behaviors (Peeters 1962), attempted copulation, and courtship or territorial flights; the latter were observed only in June. Courtship activities were observed most commonly in late July and early August and corresponded with the first influx of juvenile band-tailed pigeons at mineral sites.

Nesting Phenology

We collected 164 band-tailed pigeons from May to September in 1976 and 1977; 85 in 1976 and 79 in 1977. Of the combined collection, 68 were ASY females, 76

Table 3. Sex ratios of adult band-tailed pigeons trapped at three mineral sites in the early morning (<0900 h) and late morning (>1000 h) periods, western Oregon, 1974–76.

Interval	< 0900 h		>1000 h		Totals	
	N	Females: male	N	Females: male	N	Females: male
15–30 June	19	0.36:1			19	0.36:1
1–15 July	54	0.10:1	57	5.33:1	111	0.91:1
16–31 July	61	0.02:1	79	3.39:1	140	0.79:1
1–15 August	106	0.05:1	135	6.50:1	241	1.03:1
16–31 August	113	0.15:1	84	1.90:1	197	0.55:1
Totals	353	0.10:1	355	3.80:1	708	0.79:1

Table 4. *Percent of time spent in different behaviors by band-tailed pigeons at three mineral sites in western Oregon, 1975–76.*

Behavior	Observations	
	N	%
Feeding	386	1.8
Loafing	8,924	42.4
Courtship and mating	144	0.7
Consuming mineral	1,890	9.0
Preening	9,686	46.1
Totals	21,030	100.0

were ASY males, 12 were SY females and 8 were SY males. The sex ratios of both age classes were not different from 1:1 ($\chi^2 = 1.35$, $df = 2$, $P > 0.05$). Of the 144 ASY pigeons collected, 74 had active crop glands, but only 3 of 20 SY adults had active crop glands (Table 5). Although the sample was small, apparently fewer SY than ASY adults were reproductively active (approximately one-third, 15 versus 51%; $\chi^2 = 10.6$; $df = 1$; $P < 0.05$).

Among adult band-tailed pigeons, active crop glands were observed first in early June (Table 5). The presence of active crop glands increased until mid-July, when about 60% of the adults had active crop glands, and remained at that level until late August. However, the largest proportion of band-tailed pigeons with active crop glands was observed in the late August–early September collection period (74%).

Seasonal distribution of crop gland activity revealed that fledging of young peaked in mid-August but young continued to be fledged through September (Fig. 4). Approximately one-third of the young were fledged after

the hunting season began on 1 September. The analysis of fledging phenology by examining evidence of specific reproduction events was based on a small sample, but the pattern of fledging was similar to that obtained from crop gland activity: a peak in mid-summer with nesting activity continuing through mid-September (Fig. 5). SY females may have a later nesting phenology than adult females, although the sample size was too small to warrant a firm conclusion.

At mineral sites juvenile band-tailed pigeons were first observed in late June and increased in proportion throughout the summer, although at different rates at the three sites ($F = 61.2$, $df = 2, 30$, $P < 0.05$; comparison of slopes of regression of $\arcsin \sqrt{\%}$ juveniles by weekly periods; slopes compared by analysis of covariance); the lowest rate of increase was at site C in the Coast Range Mountains. The highest rate of increase was at the un-hunted site A (Fig. 6). The highest proportion of juveniles was in the last week in August (Site C) or the first week in September (Site A), but at Site B it was in late July and late August. Observations were terminated at sites B and C on 31 August because hunting began on 1 September. At site A, the proportion of juveniles declined slightly after the first week in September, but was still higher than at any time previous to September. From this analysis we inferred that fledging reached a peak in mid- to late August and continued at a high rate until mid-September.

We also calculated the temporal distribution of fledging using wings collected in our mail survey in 1974–76. There were no differences (2-way ANOVA; $F = 0.58$; $df = 7, 272$; $P > 0.05$) between mean dates of fledging among years (Table 6), nor between mean fledging dates among six regions in western Oregon (Table 7). Apparently the phenology of nesting varied little annually in western Oregon. The temporal distribution of fledging

Table 5. *Incidence of active crop glands at 2-week intervals, May to September in adult (1+ years-old) and yearling (1 year-old) band-tailed pigeons collected in western Oregon, 1976–77.*

Dates	Adult			Yearling		
	Sample N	Active crop glands		Sample N	Active crop glands	
		N	%		N	%
19 May–1 June	2	0	0	2	0	0
2–15 June	21	5	24	1	0	0
16–29 June	12	4	33	5	1	20
30 June–13 July	19	6	32	5	0	0
14–27 July	19	11	58	3	0	0
28 July–10 August	12	7	58	0		
11–24 August	17	10	59	2	0	0
25 August–7 September	42	31	74	2	2	100
Totals	144	74	51	20	3	15

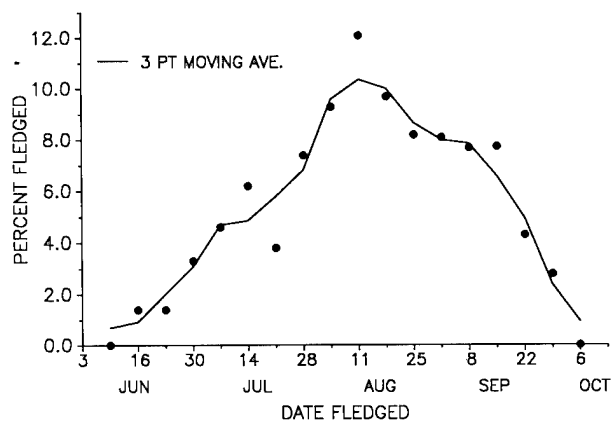


Fig. 4. Estimated fledging curve calculated from stages of development in crop gland activity of adult (AHY) band-tailed pigeons collected in western Oregon 1976-77 ($N = 88$).

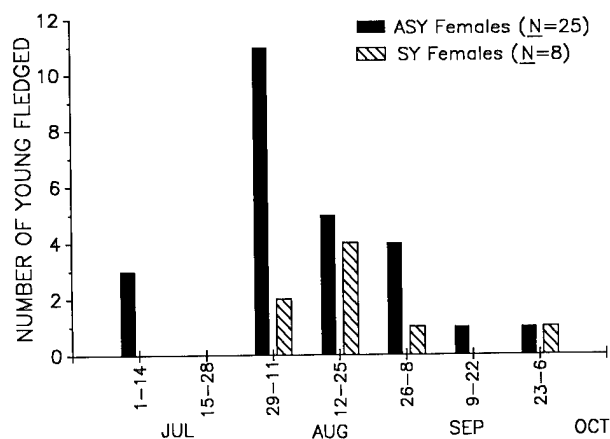


Fig. 5. Number of juveniles fledged by 2-week periods based on specific reproduction events of SY and ASY adult band-tailed pigeons collected in western Oregon, 1976-77.

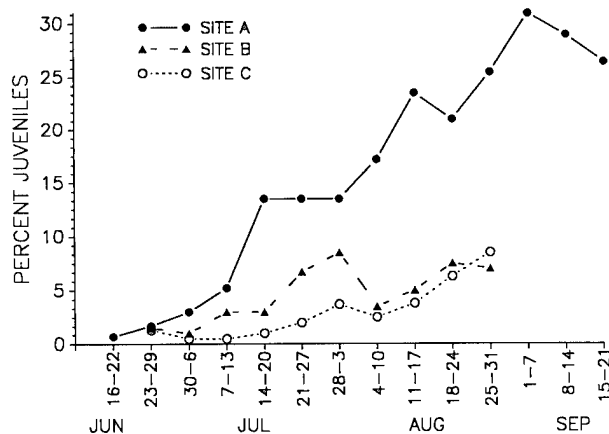


Fig. 6. Percent juvenile band-tailed pigeons observed at three mineral sites in western Oregon, 1975-76.

calculated from wings of juveniles was nearly identical to that calculated from activity of crop glands of adults (Figs. 4 and 7). In both calculations, the first young fledged in late spring (May), the peak of fledging took place in mid-August, and young continued to be fledged through September.

The distribution of fledging calculated from wings of juveniles harvested by hunters probably underestimated the rate of fledging of young in September because of reduced availability of juveniles to hunters and because of our inability to estimate fledging dates of late-hatched young (<47 days old). First, more wings were collected in the early part of the hunting season than in latter portions (1974-76 average, 1st week = 58.9%, 2nd week = 19.0%, 3rd week = 13.0%, 4th week = 8.8%), and young fledged in September had a lower probability of being bagged and collected by us than those fledged before September, both because they were available to hunters for only part of the hunting season and because fewer pigeons were bagged in the latter portions of the season. Second, the first primary is molted 23 days after fledging. Therefore, the exact date of fledging of juveniles fledged after 1 September could not be calculated for those birds shot before 23 September. By 23 September sample sizes were small. We partly alleviated this bias by assuming that all juveniles that had not molted any primaries fledged 12 days (approximate mid-point from fledging to molt of first primary) before being shot.

Table 6. Mean fledging dates and modal week of fledging of juvenile band-tailed pigeons harvested by hunters in western Oregon, 1974-76.

Year	N juveniles	Mean date	SE (days)	Mode (N fledged)
1974	128	27 July	2.5	5-11 August (25)
1975	34	31 July	4.0	not identifiable
1976	118	1 August	3.0	19-25 August (18), 5-11 August (16)

Table 7. Mean fledging dates of juvenile band-tailed pigeons harvested by hunters in six regions in western Oregon, 1974-76.

Area	N Juveniles	Mean date	SE (days)
North coast	43	31 July	4.43
Central coast	58	27 July	3.96
South coast	65	27 July	3.23
North valley	43	2 August	4.42
South valley	29	1 August	5.74
South interior	42	4 August	5.15

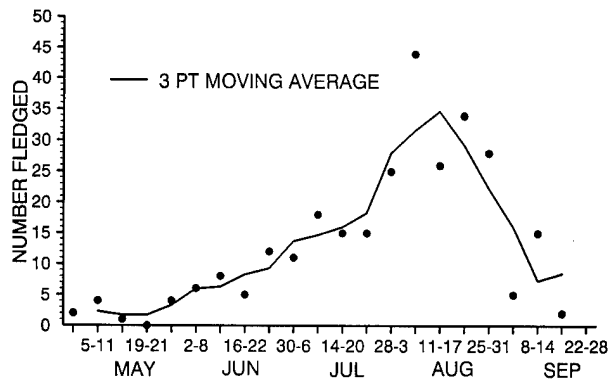


Fig. 7. Fledging curve of juvenile band-tailed pigeons based on ages calculated from wings received from hunters in western Oregon during September 1974–76 ($N = 280$).

Even with this assumption, only juveniles shot after 12 September could be identified as fledging after 1 September. Over half of our sample was collected before 12 September. Despite these shortcomings, we believe the fledging distribution generated from hunter-harvested juveniles portrayed the overall pattern of fledging of band-tailed pigeons in Oregon through mid-August. However, we believe that the rate of fledging of young did not decrease as rapidly in late August and September as depicted by the analysis of hunter-harvested juveniles.

All four methods point to a similar phenology of nesting: most young fledge from June through September. That phenology of fledging would indicate a nesting season (egg laying through fledging) of May through September, a nesting season similar to that reported for British Columbia (March and Sadleir 1970). However, earlier reports indicated a nesting season that terminated in late July or August (Gabrielson and Jewett 1940; Einarson 1953). The presence of active nests in September and

October (Hagenstein 1936; Jewett 1941) was apparently considered unusual. We judge that late summer nesting is normal for band-tailed pigeons in Oregon, and probably throughout the Northwest.

Food

Band-tailed pigeons consumed few types of food in Oregon, at least from June to September (Table 8). Berries of Pacific red elder (*Sambucus callicarpa*) was the predominant food consumed from late June to mid-August; in late August and early September, cascara buckthorn (*Rhamnus purshianus*) berries were the principal food of band-tailed pigeons. Pacific red elder berries consumed in early June were not ripe, but after mid-June only ripe berries were eaten. Thus, in Oregon, pigeons fed extensively on berries during the nesting season.

Before mid-June band-tailed pigeons apparently fed on a variety of foods, although our sample was too small to allow firm conclusions about the relative contribution of specific food items to their diet. Several observations led us to believe that, until Pacific red elder berries became readily available in mid-June, widespread movement in search of other foods was the principal activity of the pigeons. Band-tailed pigeons were attracted easily to trap sites with grain in April and May, and readily, for band-tailed pigeons, descended to the ground to consume grain. Although large numbers (ca 500) congregated at our trap site throughout April and May, numbers dwindled rapidly in June, and by mid-June trapping operations were halted because the pigeons were no longer attracted to bait. From mid-June through September, foraging band-tailed pigeons were concentrated at patches of elder and cascara buckthorn. Baiting was futile during the summer. We attempted several times to bait the pigeons at mineral sites, but they ignored grain although they would descend to the ground to consume minerals. The ease with which band-tailed pigeons were attracted to grain baits in April

Table 8. Percent occurrence of food items in crops and gizzards of band-tailed pigeons collected in western Oregon, 1976–77.

Interval	N	Elderberry	Cascara	Cherry	Grain	Misc.
19 May–1 June	4	0	0	0	75	25
2–15 June	15	27	0	27	80	13
16–29 June	17	41	0	18	53	12
30 June–13 July	24	88	0	25	0	0
14–27 July	22	91	14	14	0	5
28 July–10 August	11	91	9	18	0	0
11–24 August	17	41	71	0	0	6
25 August–7 September	31	23	90	3	0	0
Total	141					
Weighted means		53.9	51.2	13.5	17.0	5.0

and May, their disdain of grain baits after mid-June, and their extensive consumption of a few types of berries during summer, indicated that food was scarce in spring but abundant from mid-June through September.

Homing

Band-tailed pigeons displayed a strong tendency to use the same mineral sites throughout the summer. Of 284 band-tailed pigeons tagged at site C, none was observed at sites A or B in the same year they were tagged. Also, no band-tailed pigeons tagged at sites A and B were observed at site C during the same year they were tagged. However, 23% (1974) and 41% (1975) of the pigeons tagged at site A were observed one or more times at site B during the summer they were tagged. Likewise, 71% (1974), 60% (1975) and 50% (1976) of the band-tailed pigeons tagged and observed at least once at site B were subsequently observed at least once at site A during the summer in which they were tagged. These two sites were only 5.6 km apart, and band-tailed pigeons moved freely between them. Nonetheless, lack of exchange between sites A and B and site C, which was approximately 40 km from sites A and B, could indicate that band-tailed pigeons restricted their use to one, or several adjacent, mineral sites during a summer.

Changing of home sites between years was infrequent. Instances of changes between sites A and B could not be determined because it was difficult to assign a home site to band-tailed pigeons at those two sites. Three adult females tagged at site C in 1975 were consistently observed at site A in 1976, and an adult female tagged at site A in 1974 was observed once at site C in 1975. An adult male tagged at site B in 1974 and observed twice in 1974 at site B was observed at a feeding station in Kent, Washington, in May, September, and October 1976 (C. F. Martinson, personal communication). Finally, an adult female tagged in 1975 at site C was observed in June 1976 near Salem, Oregon. Thus, movement among mineral sites took place, but infrequently.

Band-tailed pigeons displayed a strong tendency to return to the same mineral site used in previous years. To

calculate homing rates, we first needed to calculate correction factors to account for band-tailed pigeons that lost their tags during the interval from tagging to observation. We used a binomial probability function applied to the number of reobserved birds retaining one and two tags to estimate the number retaining no tags.

Of the birds marked in 1974, 22 were observed in 1975; 19 retained one tag and 3 retained two. Probability of losing a single tag was 0.76, resulting in a correction factor of 2.37. In 1976, nine birds tagged in 1974 were observed; six retained one tag and three retained two tags. Probability of losing a tag from 1974 to 1976 was 0.50, resulting in a correction factor of 1.33. Also in 1976, 96 birds tagged in 1975 were observed; 64 retained two tags and 32 retained one tag. Probability of losing a tag was 0.20, resulting in a correction factor of 1.04. The high rates of loss of tags from birds banded in 1974 resulted from the nylon fastener; a stainless steel fastener was used in 1975.

Overall rates of return were fairly high (\bar{x} = 66%; Table 9). Females returned at a higher rate (\bar{x} = 74%) than males (\bar{x} = 62%) but return rates were quite variable among years. These return rates are probably only approximations at best as several calculated rates were greater than 100%, and were based on small samples. The 1975–76 rates, based on larger samples, are the better estimates. However, mean rates may be biased low because both the correction factor and return rates were estimated by assuming that all tagged birds present were observed, an assumption that was probably violated.

We conclude that most surviving adult band-tailed pigeons used a single, or several adjacent, mineral sites throughout their lives. Thus, band-tailed pigeons associated with a mineral site formed discrete subunits within the breeding population.

Migration

Many researchers (Grinnell 1913; Neff 1947; Smith 1968; Silovsky 1969) suggested that bandtails begin their fall migration in late August and early September, and that nearly all bandtails leave Oregon by October. Those

Table 9. Calculated return rate by adult band-tailed pigeons in subsequent years to mineral site where originally trapped in western Oregon, 1974–76. *N* is the number reobserved.

Year		Males		Females		Totals/means ^a	
Tagged	Observed	<i>N</i>	%	<i>N</i>	%	<i>N</i>	%
1974	1975	13	115	6	140	19	122
1974	1976	5	39	3	62	8	45
1975	1976	40	49	28	62	68	54
Totals		59		37		95	
Weighted means^a			62		74		66

^a Weighted mean based on sample size.

Table 10. *Temporal distribution (%) of 836 recoveries of adult band-tailed pigeons banded at four sites in western Oregon, 1950–78.*

Recovery	Banding sites (North latitude)				All sites combined (N = 836)
	40°50' (N = 151)	44°30' (N = 198)	45°20' (N = 158)	45°40' (N = 329)	
September					
1–5	53.0	47.5	42.4	50.2	48.6
6–10	21.8	18.7	24.7	24.3	22.6
11–15	10.6	21.2	15.2	12.2	14.6
16–20	9.3	7.6	8.9	9.1	8.7
21–25	4.0	4.0	6.3	2.7	4.0
25–30	1.3	1.0	2.5	1.5	1.6

suggestions were based on general observations of unmarked birds rather than on quantitative data on movements of marked birds.

We analyzed reports from 836 band-tailed pigeons recovered between 1950 and 1978 to assess initiation of fall migration. These individuals met the following qualifications: banded in spring, recovered in September (hunting season recoveries) with date of recovery reported, and recovered in Oregon, Washington, and British Columbia with locality of recovery reported. Hunting seasons were concurrent (1–30 September) in Oregon, Washington, and British Columbia from 1950 to 1978, the period during which we examined recoveries. Recoveries were recorded by 5-day periods during the hunting season and by distance (degrees latitude north or south) from banding site. Nearly all recoveries were within a 2° longitudinal band along the Pacific Coast, therefore longitudinal distance from banding sites was disregarded. We reasoned that if migration took place during September, proportionately more recoveries should take place south of the banding site as the hunting season progressed, as compared with recoveries from the banding site and areas north of it. To test that hypothesis statistically,

considerable pooling and preliminary testing of data was necessary.

Of the 836 recoveries, 354 were direct (recovered in calendar year banded) and 482 were indirect (recovered at least 1 calendar year after banding). The recoveries did not differ in either temporal (5-day intervals; $\chi^2 = 4.29$, $df = 5$, $P > 0.05$) or spatial (1° latitudinal intervals; $\chi^2 = 9.02$, $df = 8$, $P > 0.05$) distribution, therefore, direct and indirect recoveries were pooled.

Most birds (99.6%) were banded at four sites but temporal distribution was not different ($\chi^2 = 18.9$, $df = 15$, $P > 0.05$; Table 10) among birds banded at the four sites. However, spatial distribution of recoveries was different ($\chi^2 = 65.8$, $df = 18$, $P < 0.05$; Table 11). Much of the difference in spatial distribution of recoveries among sites was caused by deviation from expected number of recoveries at the farthest distances from banding sites ($>2^\circ$ south and $>3^\circ$ north, Table 11), where numbers of recoveries were small. Also the clumped distribution of recoveries around the banding site at $45^\circ 40'$ N latitude contributed to the large χ^2 value obtained. Because of the need for large sample sizes to analyze spatio-temporal distribution of recoveries, and

Table 11. *Spatial distribution (%) of 836 recoveries of adult band-tailed pigeons banded at four sites in western Oregon, 1950–78.*

Degrees from banding site	Banding sites (North latitude)				All sites combined (N = 836)
	43°50' (N = 151)	44°30' (N = 198)	45°20' (N = 158)	45°40' (N = 329)	
$\geq 2^\circ$ S	1.3	3.5	8.9	3.0	4.0
1° S	8.0	6.6	10.1	2.4	5.9
0	72.8	63.6	61.4	79.3	71.1
1° N	4.6	11.6	7.0	7.0	7.7
2° N	2.6	8.1	7.6	4.6	5.6
3° N	4.0	3.5	5.1	2.7	3.6
$\geq 4^\circ$ N	6.6	3.0	0	1.0	2.3

Table 12. *Spatiotemporal distribution (%) of 836 recoveries of adult band-tailed pigeons banded in spring in western Oregon, 1950-78.*

Degrees from banding site	September						Means (N = 836)
	1-5 (N = 406)	6-10 (N = 189)	11-15 (N = 122)	16-20 (N = 73)	21-25 (N = 33)	26-30 (N = 13)	
≥2° S	3.9	2.7	3.3	1.1	9.1	23.1	4.0
1° S	4.9	5.8	9.8	4.1	0	23.1	5.9
0	72.2	76.2	65.6	68.5	72.7	23.1	71.1
1° N	8.9	5.8	7.4	5.5	9.1	7.7	7.7
2° N	4.7	6.4	5.7	8.2	6.1	7.7	5.6
3° N	5.4	3.2	8.2	11.0	3.3	15.4	5.9

because we do not believe that differences in spatial distribution among banding sites seriously compromised the analysis, we combined recoveries from all banding stations in Oregon.

Testing the combined samples, we were unable to detect a southerly shift in recoveries as the hunting season progressed (Table 12). The temporal distribution of recoveries (by 5-day periods of the hunting season) did not differ at increasing distances (degrees latitude north and south of the banding sites) from the banding sites ($\chi^2 = 28.29$, $df = 20$, $P > 0.05$). However, there was a slight numerical increase in the proportion of recoveries south of the banding site near the end of September (Table 12). This numerical increase was most apparent during the last 5 days of September but because of small sample sizes, the statistical analysis was conducted on a truncated matrix that combined the last two, 5-day periods. We concluded that no major migratory movement took place before 20 September.

Of band-tailed pigeons banded in Washington, 278 recoveries met the criteria for selection. These recoveries had a different ($\chi^2 = 94.7$, $df = 7$, $P < 0.05$) spatial distribution, relative to the site of banding, than birds banded in Oregon and thus could not be combined with recoveries of birds banded in Oregon. However, the spatial distribution of these 278 birds did not change ($\chi^2 = 23.9$, $df = 16$, $P > 0.05$) as the hunting season progressed (Table 13). The numerical pattern of recoveries

was ambiguous, both increasing and decreasing south of the banding site as the hunting season progressed. This test, as was the case for birds banded in Oregon, failed to yield any indication of migration in September.

These analyses probably have only modest capability of detecting migratory movements of band-tailed pigeons in September, particularly in the latter half of the month. Differences in the likelihood of hunters encountering resident and migrating band-tailed pigeons would bias the distribution of recoveries we examined. Hunting activity was not equally distributed at mineral sites, feeding areas and flyways, but the presence of resident versus migrating band-tailed pigeons at those three areas was unknown. We have no basis for estimating the likelihood of hunters encountering resident versus migrating band-tailed pigeons but recognize this problem potentially weakens the conclusion that migration did not take place before late September.

The number of recoveries declined rapidly during September with nearly 50% taking place in the first 5 days of the month and about 5% in the last 10 days (Table 10). This rapid decline in recoveries could be caused by migration of band-tailed pigeons, as Silovsky (1969) concluded, but the temporal distribution of hunters and pigeons is inextricably confounded. Therefore, we believe that a conclusion of migration from the numerical decline of recoveries is unwarranted.

The fall migration of pigeons in Oregon and Wash-

Table 13. *Spatiotemporal distribution (%) of 278 recoveries of adult band-tailed pigeons banded in western Washington, 1950-78.*

Degrees from banding site	September					Means (N = 278)
	1-5 (N = 124)	6-10 (N = 75)	11-15 (N = 35)	16-20 (N = 25)	20-30 (N = 19)	
3-5° S	12	15	9	28	21	12
1-2° S	20	21	20	28	5	20
0	47	48	60	32	58	48
1-4° N	27	16	11	12	16	20

ington has been described as large flocks moving slowly southward whereby the "...birds 'feed' their way along, the roosting place each evening lying farther south than that of the night before" (Neff 1947). This migration "...in Oregon normally begins during the last days of August and is well completed by September 20" (Neff 1947). Our analyses of band recoveries should have detected those types of movements: large numbers of birds moving southward daily in early September. Perhaps Neff (1947) observed premigratory movements because he also reported that "After the major breeding season, pigeons flock together and move about locally following successions of food crops." However, Neff and his colleague (Einarsen 1953) were astute observers, and their descriptions of migration cannot be dismissed lightly. Nonetheless, our quantitative analysis of movements of marked birds lends credence to our view that autumn migration did not begin before late September. Additional study using radiotelemetry will be necessary to resolve the question of timing of fall migration of band-tailed pigeons.

Most recoveries (61–79%) took place in the same degree of north latitude in which banding sites were located (Table 11). Apparently many band-tailed pigeons remained in the general vicinity of the banding site from time of banding in spring to September and many also returned in subsequent years to the same locale. Contrary to the assumptions of some (Mace and Batterson 1961; Wight et al. 1967; Silovsky 1969) that band-tailed pigeons trapped in spring were migrants, our analysis indicated that the pigeons established residency in early spring, remained through September, and had a high affinity for the same area in subsequent years.

Age Structure of the Population

Recruitment of Young

Obtaining reliable estimates of the percent juveniles recruited into the population was difficult because some young fledged after hunting commenced, hunting disrupted observations, trapping at mineral sites ceased before all young were fledged, and too few young were banded to provide estimates of direct recovery rates. However, we obtained information on percent juveniles observed at mineral sites before 1 September and on percent juveniles shot by hunters.

About 17% of the band-tailed pigeons shot by hunters were juveniles (Table 14). The proportion of the harvest composed of juveniles varied little annually ($\chi^2 = 5.96$, $df = 5$, $P > 0.05$). The percent of harvest composed of juvenile band-tailed pigeons may not be an accurate estimate of recruitment because young and adults probably had different probabilities of being harvested by hunters. Juveniles of most game birds are more vulnerable to hunting than adults and percent juveniles in the

Table 14. *Percent of hunter kill composed of juvenile band-tailed pigeons in western Oregon, 1966–67 and 1973–76.*

Year	N wings examined	Percent juveniles
1966	1,361	16.5 ^a
1967	1,672	18.6 ^a
1973	579	18.3
1974	861	15.0
1975	211	17.1
1976	707	16.8
Total Mean	5,391	17.1

^aFrom Silovsky (1969).

harvest produces an overestimate of recruitment. We were unable to test for this potential bias with relative recovery rates (Hickey 1952) because too few juvenile band-tailed pigeons were banded and recovered. However, percent juveniles in the harvest can be used as an index to recruitment provided the relative rates at which adults and juveniles were shot by hunters did not vary among years. We were unable to test this assumption but we think it was valid. We conclude that recruitment did not vary annually.

Percent juveniles shot by hunters increased as the hunting season progressed (Table 15). Although there was some variability among years, probably as a result of small sample sizes, percent juveniles shot by hunters increased from a low of 12.5% during the first 5 days of September to 24% by mid-September and remained slightly below that level for the remainder of the season. We detected no migration of adults in September.

Juvenile band-tailed pigeons harvested by hunters became progressively younger (later date of fledging) as the hunting season advanced during September (slope = 0.676, $r = 0.19$, $P < 0.05$; Fig. 8). Fledging of young in September would decrease the average age of the juvenile segment of the population available to hunters during September. However, if migration of juvenile band-tailed pigeons was a function of age, early departure of older juveniles through migration from Oregon would also reduce the average age of the remaining segment of juveniles available to hunters as the hunting season progressed in September. If that scenario was correct, a positive relation between date of harvest and date of fledging for those juveniles fledged before 1 September would be expected. Least squares analysis showed no relation between date of harvest and date of fledging for juveniles fledged before 1 September (slope = -0.15, $r = 0.04$; $P > 0.05$), which suggests that older juveniles did not migrate earlier than younger juveniles. We con-

Table 15. *Percent of harvest composed of juvenile band-tailed pigeons in western Oregon by 5-day periods of the hunting season, 1973–76.*

Period	1973		1974		1975		1976		Totals	
	N	% Juv	N	% Juv	N	% Juv	N	% Juv	N	% Juv
September										
1–5	319	15.6	435	12.2	88	6.8	275	11.6	1,117	12.5
6–10	123	17.1	151	19.2	44	18.2	125	10.5	443	16.0
11–15	56	25.0	115	20.0	41	31.3	102	27.5	314	23.9
16–20	35	14.3	46	13.0	17	29.4	93	20.3	191	18.3
21–25	28	35.7	72	9.7	17	41.2	51	25.5	168	22.0
26–30	18	38.9	37	16.2	4	0	26	23.1	85	22.4
Totals	579		856 ^a		211		672 ^a		2,318	
Weighted means		18.3		14.5		17.1		16.5		16.3

^aTotals differ from those in Table 14 because date of harvest was unknown for some birds.

clude that juveniles were being added to the population by recruitment during September and that recruitment accounted for both the increasing proportion of juveniles in the population and the decreasing average age of the juvenile segment of the population. This conclusion is consistent with observations of reproduction activity continuing well into September and migration not beginning before late September.

The percentage of band-tailed pigeons observed at mineral sites that were juveniles varied considerably among the three sites we studied (Fig. 6), but variation among years at each site was negligible. During the last week in August the percentage of band-tailed pigeons that were juveniles varied from 7 to 8.5% at sites B and C but was about 25% at site A. Percentage of young increased to about 30% in September at site A and remained at that level until near the end of September.

Activities of hunters precluded observations of pigeons at sites B and C in September. The differences among sites were large and not obviously related to any factors we could discern.

The proportion of juveniles observed at mineral sites may not be a reliable estimate of recruitment. Juvenile band-tailed pigeons only rarely attempted to consume minerals while at the sites and possibly congregated at mineral sites in response to social stimuli. Adult band-tailed pigeons seemingly were attracted to minerals at the sites to fulfill calcium requirements associated with reproduction (March and Sadleir 1975). Tagged juveniles visited the sites at a greater frequency (0.150 visits per day per tagged individual) than adults (0.078; Table 16), but the sample of juveniles was small (12). Kautz (1977) noted large differences in the proportion of juveniles at feeding sites and thought that differences in activity pat-

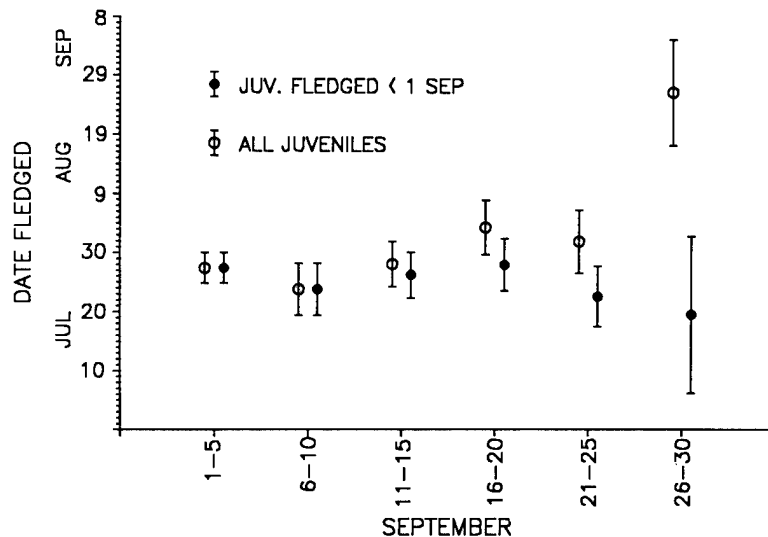


Fig. 8. Mean (\pm SE) fledging dates of band-tailed pigeons for all juveniles, and for juveniles fledged before 1 September, based on wings received from hunters in western Oregon, 1974–76. Vertical bars = \pm 1 SE.

terns resulted in nonrandom distribution in time and space of juveniles among adults. Differential frequency of appearance of adults and juveniles would cause age ratio information from mineral sites to overestimate recruitment rates. This may be especially true of the 25–30% juveniles observed at site A, but the 7–8% observed at sites B and C seems incongruously low.

We suggest recruitment of juvenile band-tailed pigeons was between the 15–18% derived from hunter-harvested birds and 25–30% present at mineral site A in mid-September. However, we are unsatisfied with our explanations of the low percent of juveniles observed at sites B and C, and are concerned that we may have overestimated recruitment.

Proportion of Second-Year Band-tailed Pigeons

We generated estimates of the proportion of SY birds in the population from four independent sources: band-tailed pigeons trapped in May and June, trapped at mineral sites in July and August, collected from June to September, and shot by hunters in September.

Age was ascertained for band-tailed pigeons banded in May and June only during 1968–69 and 1976–77. SY band-tailed pigeons composed 8.8 to 17.0% of adult band-tailed pigeons trapped during those years (Table 17); differences between years were significant ($\chi^2 = 21.4$, $df = 3$, $P < 0.05$). In addition, the proportion of SY birds was not constant throughout the spring banding period (Table 18). Fewest SY pigeons were banded in early May, but the percentage steadily increased until late May and remained nearly constant until banding ceased in mid-June. The initial low percentage of SY pigeons banded suggested that ASY adults migrated north earlier than SY birds. However, high percentages of SY pigeons banded in late May and June may be biased upwards because ASY band-tailed pigeons began nesting earlier than SY birds (Fig. 5). If nesting birds fed on berries and ceased to feed on grain (bait), as indicated by food habits and nesting chronology, the number of adults

Table 16. Daily observation rates^a of tagged band-tailed pigeons (number observed per day per tagged bird) at three mineral sites in western Oregon, 1975.

Site	Adults		Juveniles	
	N tagged pigeons	Daily observation rate	N tagged pigeons	Daily observation rate
A	67	0.090	9	0.187
B	48	0.056	2	0.107
C	51	0.079	1	0.026
Totals	166	0.078	12	0.150

^aRates based on tagged pigeons observed at least once after tagging.

Table 17. Age classes of band-tailed pigeons captured in spring (May–June) at Corvallis, Oregon, 1968–69 and 1976–77.

Year	N ^a	Percent	
		ASY Adults (1+ years-old)	SY Adults (1 year-old)
1968	1,074	86.8	13.2
1969	666	83.0	17.0
1976	658	91.2	8.8
1977	392	83.9	16.1
Total Mean	2,790	86.2	13.8

^aOnly data from annual initial captures of individuals were used.

at our baited trap site would have declined. Thus, the percentage of SY band-tailed pigeons captured would have been inflated compared to the percentage present in the population.

At mineral sites, SY birds composed 14% (Table 19) of birds banded, excluding juveniles. There were no differences among sites ($\chi^2 = 1.9$, $df = 2$, $P > 0.05$) but significantly more SY band-tailed pigeons were trapped in 1974 than in 1975 and 1976 ($\chi^2 = 21.1$, $d.f. = 2$, $P < 0.05$). Of 164 band-tailed pigeons, excluding juveniles, collected from May to September, 1976–77, 20 (12.2%) were SY birds.

Contrary to the preceding estimates, a small percent of AHY band-tailed pigeons shot by hunters was classified as SY (1.3%). We believe this estimate was biased. SY birds retained only a few buff-tipped coverts, and those most likely to be diagnostic were the innermost

Table 18. Age classes of band-tailed pigeons captured in spring at Corvallis, Oregon, grouped by 5-day periods, 1968–69 and 1976–77.

Interval	N ^a	Percent	
		ASY Adults (1+ years-old)	SY Adults (1 year-old)
1–5 May	305	95.4	4.6
6–10 May	269	94.8	5.2
11–15 May	272	94.5	5.5
16–20 May	258	86.0	14.0
21–25 May	356	74.6	26.4
26–30 May	505	84.5	15.5
31 May–4 June	533	83.3	16.7
5–9 June	270	87.8	12.2
10–14 June	22	86.4	13.6
Total Mean	2,790	86.2	13.5

^aOnly data from annual initial captures of individuals were used.

Table 19. *Percent of band-tailed pigeons (excluding juveniles) trapped at three mineral sites in western Oregon during July and August, 1974–76, that were SY adults (1 year-old).*

Year	Mineral site						Totals	
	A		B		C			
	N ^a	Percent	N ^a	Percent	N ^a	Percent	N ^a	Percent
1974	74	24.3	70	32.9	85	12.9	229	22.7
1975	122	10.7	90	5.6	156	10.9	368	9.5
1976			46	8.7	21	14.3	67	10.5
Totals	196		206		262		664	
Weighted means		15.8		15.5		11.8		14.2

^aOnly data from annual initial capture of individuals were used.

secondary covert feathers (tertial coverts). Wings sent to us by hunters were often bedraggled and frequently the innermost secondaries and accompanying coverts were missing. We suspected that many SY birds were classed as ASY. Consequently, we rejected the proportion of SY band-tailed pigeons shot by hunters as a valid estimate of the proportion of SY birds in the breeding population.

The proportion of SY band-tailed pigeons we identified probably was an underestimate of the actual proportion present in the population. A few SY birds cannot be recognized because they have molted all juvenal coverts and primaries by spring. We used White's (1973) criteria of age from 1975 to 1977, but the criteria of Silovsky et al. (1968) were used before 1975. Nonetheless, proportions of SY birds before and after 1975 varied little. Thus we used White's maximum estimate (20%) of the unidentified SY band-tailed pigeons present in our samples.

The unweighted mean proportion of SY band-tailed pigeons in our samples was 12.5% (min–max 9–17%). This value indicated that the breeding segment of the population was composed of 15.6% (0.125/0.80) SY birds (min–max 11–21%). Because juvenile band-tailed pigeons composed 15–30% of the fall population, SY birds composed 10.9 (0.156 × 0.70) to 13.3% (0.156 × 0.85) of the entire population in fall (assuming equal mortality of SY and ASY birds during summer). By use of median values, the fall population would consist of 23% juveniles, 12% SY and 65% ASY birds, with a range of 15–30% juveniles, 11–13% SY and 57–74% ASY. The spring breeding population, based on median values, contained about 16% SY and 84% ASY band-tailed pigeons.

Survival

From 1950 to 1977, 23,086 AHY band-tailed pigeons were banded during spring (April–June) in western Oregon (Table 20). Banding was conducted at four principal locations: three in coastal areas from Reedsport to Nehalem (43°50' to 45°40' North latitude) and one at

Corvallis (44°30' North latitude). The sex of many birds was not recorded and we combined data for the two sexes for analysis. From these bandings, 1,554 bands

Table 20. *Banding and recovery of adult (AHY) band-tailed pigeons.^a*

Year	N banded	N recovered	Oldest recovery (years after banding)
1950	35	8	11
1952	112	10	22
1953	533	56	13
1954	778	75	11
1955	464	39	12
1956	1,222	110	11
1957	590	57	14
1958	214	17	9
1959	84	6	11
1960	498	34	11
1961	154	9	6
1962	259	21	10
1963	166	3	14
1964	389	24	7
1965	642	39	12
1966	1,637	130	11
1967	2,791	140	10
1968	3,373	206	9
1969	1,585	100	9
1970	2,428	174	7
1971	1,763	145	6
1972	1,362	74	7
1973	500	23	6
1974	5	0	
1975	491	27	3
1976	619	21	3
1977	92	6	2
Totals	23,086	1,554	

^aBirds were banded in spring in western Oregon and recovered during the hunting season.

were recovered during the hunting seasons from 1950 to 1979. Pigeons were recovered up to 22 years after banding; the average interval between banding and recovery was 2.6 years for birds banded from 1950 to 1973.

Annual estimates of survival varied from 9.4 to 369% from 1950 to 1976; small sample sizes in many years resulted in imprecise estimates. Consequently, our estimates were based on the 16,081 band-tailed pigeons banded from 1965 to 1973. During those years survival estimates varied from 44.5 to 85.3% and averaged 63.7% (95% CI = +7.6%; Table 21). The recovery distribution fit the model ($\chi^2 = 36.4$, $df = 38$, $P > 0.05$). Annual estimates of survival were fairly imprecise (95% CI from +12.0 to +25.5%) but the mean survival for the 1965–72 interval had a narrow confidence interval (+7.6%). Thus, we used the mean survival rate as an estimate of average annual survival.

We were concerned that trapping affected survival of banded and released birds because birds occasionally exhibited signs of distress upon release and a few were found dead within 1–3 days of being banded. Death immediately after release would depress first-year recovery rates and estimates of survival rates. We tested the hypothesis that direct recovery rates were higher than indirect recovery rates by the method of Brownie et al. (1978). This is their test of Model I vs Model 0 and specifically tests the hypothesis that first-year recovery rates (f^*) equal recovery rates of birds banded 1 or more years previously (f_i), where i is the year in which recoveries took place. First year recovery rates ($f^* = 0.0275$) did not differ significantly from recovery rates of birds recovered 1 or more years after banding ($f = 0.0246$; $z = 2.76$, $P > 0.05$). This test does not test the possibility of depressed estimates of survival the first year after banding but, because recovery rates were not affected, we would not expect survival rates to be affected

by trapping induced mortality. Seemingly the distress we observed in banded and released birds had an inconsequential effect on survival, or at least on estimates of survival.

Wight et al. (1967) reported a survival rate of 71.3% based on recoveries of adults banded at Nehalem, Oregon from 1952 to 1965; based on returns (birds recaptured at original trapping site 1 or more years after initially banded) they estimated a survival rate of 70.9%. Silovsky (1969) estimated that survival of adult band-tailed pigeons banded at Reedsport, Oregon from 1952 to 1957 was 67.9%. Survival of adults banded in Washington (1950–65) was 62.2% and survival of adults banded in California (1952–65) was 61.1% (Silovsky 1969). Smith (1968) calculated an average annual survival of 57.3% for adult and juvenile band-tailed pigeons (combined) banded in California (1952–58).

The survival estimates reported by Wight et al. (1967), Smith (1968) and Silovsky (1969) were calculated with a composite–dynamic life table procedure (Hickey 1952). The assumptions of the composite–dynamic life table procedure are seldom met by recoveries from banded birds (Burnham and Anderson 1979; Anderson et al. 1981). Thus, comparisons of those estimates of survival with those we calculated may be inappropriate.

Braun et al. (1975) reported an average annual survival rate of 63.9% for adults and 58.3% for juveniles in the southern Rocky Mountain region. They used the relative recovery rate method (Hickey 1952) which is similar to the Brownie models, but apparently did not test the assumptions of the model, nor did they report standard errors for their estimates of survival. More recently Kautz and Braun (1981) calculated annual survival rates of 73% for adults and 66% for juvenile band-tailed pigeons banded in Colorado. These estimates were calculated with Model H_i of Brownie et al. (1978).

Table 21. *Estimated survival and recovery rates of adult (AHY) band-tailed pigeons banded during spring (April–June) in western Oregon, 1965–73.*

Year	N banded	Survival		Recovery	
		Rate	±95% CI	Rate	±95% CI
1965	642	0.445	0.193	0.0312	0.0134
1966	1,637	0.853	0.234	0.0333	0.0083
1967	2,791	0.777	0.175	0.0146	0.0038
1968	3,373	0.481	0.120	0.0191	0.0038
1969	1,585	0.659	0.160	0.0181	0.0047
1970	2,428	0.588	0.129	0.0213	0.0044
1971	1,763	0.756	0.208	0.0388	0.0072
1972	1,362	0.534	0.255	0.0357	0.0082
1973	500			0.0203	0.0090
Total	16,081				
Means		0.637	0.044	0.0265	0.0026

Population Trends

We used counts of band-tailed pigeons at eight mineral sites conducted by personnel of the ODFW to assess population trends. The numbers of pigeons counted at the eight mineral sites varied considerably among sites and among years (Table 22). However, counts were highest in the early 1960's and lowest in the early 1970's at nearly every site. The population index indicated an

increasing trend from 1950 to the early 1960's, a strong downward trend from the mid-1960's to the mid-1970's, a modest increase from the mid-1970's to the early 1980's followed by another decrease in the mid- to late 1980's (Fig. 9). The high for the population index was in 1963 and was 180% of the long-term average; the low index values were 34% of the long-term average in 1975 and 30% in 1987. The highest index value since 1975 was 83% of the long-term average in 1984. Correlation analy-

Table 22. Number of band-tailed pigeons counted at eight mineral sites in western Oregon, 1950–80.

Year	Mineral sites								Population index ^a
	1	2	3	4	5	6	7	8	
1950		224			223	300	593		1.316
1951	210	204			208	235	762		1.141
1952	390	196			163	187	714		1.138
1953	572	174			149	314	781		1.469
1954									
1955	390	322			226	151	197		1.032
1956	756	400		588	285	370	706	230	1.713
1957	675	334		275	144	302	300	307	1.315
1958	405	347	1,171	337	474	220	109	164	1.366
1959	732	324	1,191	508	422	284	314	160	1.642
1960			989	380	654		451	119	1.421
1961	791	152		855	348		737	255	1.530
1962	521	126	1,332	911	348	177	578	278	1.582
1963	114	400	488	698	356	193	933	256	1.781
1964	369	500	566	472		305	576	233	1.466
1965	502	257	949	573	708	376	617	262	1.799
1966	150	373		678	746	179	712	208	1.433
1967	44	632	870	405	274	106	752	144	1.207
1968	246	603	988	230	333	122	703	252	1.361
1969	120	190	728	258	348	125	511	63	0.889
1970	118	375	650	449	225	247	542	181	1.143
1971	169	373	505	455	314	164	497	161	1.059
1972	79	108	604	309	487	125	806	214	1.020
1973	55	93		408	151	52	227	81	0.461
1974	79	83	161	135	37	30	338	142	0.366
1975	35	62	117		102	0 ^b	88	282	0.342
1976	140	155	29	215	213	0	203	260	0.495
1977	118	55	82	192	225	0	187	357	0.553
1978	31	100	1	387	196	0	270	214	0.429
1979	118	200	0 ^b		144	0	434	493	0.660
1980	94	175	0	579	136	0	644	478	0.757
1981	212	105	0	345	235	0	694	566	0.816
1982	84	257	0		134	0	520	233	0.546
1983	48	75	0	639	121	0	731	392	0.671
1984	43	500	0	738	127	0	746	215	0.826
1985	80	325	0	439	88	0	151	48	0.424
1986	48	157	0	460	113	0	398	0 ^b	0.431
1987	10	110	0		94	0	501	0	0.301
1988		75	0	330	41	0	468	0	0.347
Mean	273.2	247.0	408.2	456.8	262.5	126.8	519.5	241.6	1.000

^aMethod of calculation of population index described in Methods.

^bCounts discontinued because of lack of band-tailed pigeons; data treated as automatic zeros.

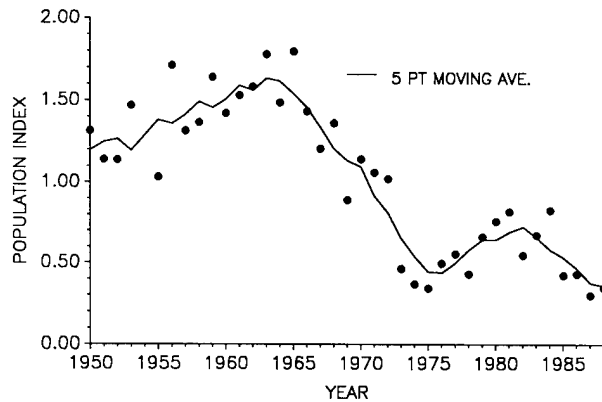


Fig. 9. Abundance of band-tailed pigeons in western Oregon 1950–88 based on counts at eight mineral sites.

sis (\ln of population index) indicated a significant ($P < 0.05$) positive relation between the index and time from 1950 to 1965 ($r = 0.69$) and from 1975 to 1984 ($r = 0.77$), and strong negative relation from 1963 to 1978 ($r = -0.90$) and from 1980 to 1988 ($r = -0.83$). These analyses show that band-tailed pigeons increased in abundance at annual rates of 2.4% from 1950 to 1965 and 7.1% from 1975 to 1984, but decreased at annual rates of 10.4% from 1963 to 1978 and 11.1% from 1980 to 1988 ($1 - e^{-\text{slope}}$).

Hunting

Harvest

The estimated annual harvest in Oregon varied from 122,000 in 1958 to 45,000 in 1987 (Table 23). Of the

Table 23. Harvest of band-tailed pigeons in Oregon, Washington, and California and number of hunters in Oregon, 1957–87.

Year	Harvest (thousands)				Hunters in Oregon (thousands)
	Oregon	California	Washington	Totals	
1957	94	255	74	423	14.6
1958	122	195	73	390	20.3
1959	86	157	90	333	13.1
1960	87	310	87	484	13.1
1961	121	233	94	448	15.0
1962	121	338	104	563	14.1
1963	90	249	93	432	16.5
1964	104	243	127	474	12.5
1965	105	207	158	470	12.6
1966	121	322	158	601	12.4
1967	82	260	109	451	9.9
1968	95	307	152	554	12.3
1969	85	216	95	396	11.3
1970	99	181	120	400	12.9
1971	84	286	130	500	10.8
1972	87	537	100	724	11.5
1973	66	272	99	437	9.6
1974	66	210	91	367	10.4
1975	64	132	82	278	10.7
1976	50	90	77	217	10.4
1977	66	107	72	245	10.3
1978	^a	135	70	^a	
1979	88	183	88	359	15.5
1980	78	133	67	278	12.6
1981	88	214	64	366	14.6
1982	83	118	55	256	12.5
1983	97	154	56	307	11.5
1984	^a	126	^b	^a	
1985	72	78			10.7
1986	51	65			9.0
1987	45				5.9
Mean	86	211	96	414	12.3

^aHarvest and hunters not estimated in Oregon in 1978 and 1984.

^bHarvest survey methodology altered beginning in 1984 and estimates not comparable to previous years.

total harvest in Washington, Oregon, and California, 1957–87, about 22% were harvested in Oregon, 23% in Washington, and 55% in California.

Although there was much annual variability in number of band-tailed pigeons harvested in Oregon, a pattern of decreasing harvest was apparent, especially since the mid-1960's (Fig. 10). Regression of harvest on year indicated that year was only a partial ($r^2 = 0.44$, $P < 0.05$) predictor of the harvest and harvest decreased by about 1500 per year. The pattern of harvest from 1957 to 1987 was similar to the pattern of the population index (Fig. 9) although the rate of decline of harvest was not as great as the rate of decline of the population index. Harvest fluctuated before 1963 whereas the population index indicated a modest increase during that period.

From 1957 to 1987 the population index, derived from counts at mineral sites, was related to harvest in Oregon ($r^2 = 0.62$, $P < 0.05$; Fig. 11). The index was weakly related to total harvest in the three coastal states

(1957–83; $r^2 = 0.30$, $P < 0.05$), harvest in California (1957–7; $r^2 = 0.24$, $P < 0.05$), and harvest in Washington (1957–83; $r^2 = 0.29$, $P < 0.05$), which made the index a poor predictor of harvest. In Oregon, the number of band-tailed pigeon hunters also was related directly to (Fig. 12) and was a fair predictor of harvest ($r^2 = 0.58$, $P < 0.05$). In a multiple regression, the population index and number of Oregon hunters both were related to harvest in Oregon and together accounted for 76% of the annual variability in harvest.

Mail Survey

Hunters returned 857 packets containing 2,391 wings during the 4 years of the mail questionnaire survey (Table 24). Each packet represented the bag during 1 day of hunting by one hunter; only successful hunters responded to the survey. The number of hunters initially contacted varied each year and depended upon the number responding to the ODFW harvest survey of the previous year. Because an unknown number of people who had hunted the previous year were unavailable to respond (change of address, deceased, etc.), and because of the annual variation in number of hunters initially contacted, the number of packets and wings received was not indicative of the size of the annual harvest of band-tailed pigeons.

The average number of band-tailed pigeons bagged per hunt, for successful hunters, varied from 3.03 in 1974 to 2.51 in 1976 (Table 24). In 1975, bag limits were reduced from eight to five pigeons per day. The average daily bag (unweighted) in 1973–74 was 2.97, and in 1975–76 was 2.53. The reduction of 0.44 birds bagged per day indicated that successful hunters bagged 14.4% fewer birds following the reduction in bag limit in 1975. The estimated total harvest averaged 63,000 per year in 1973–74 and 56,900 per year in 1975–76, a reduction of 9.7%. Our data on the average number of band-tailed pigeons bagged per trip does not account for differences in the number of hunting trips per year, the

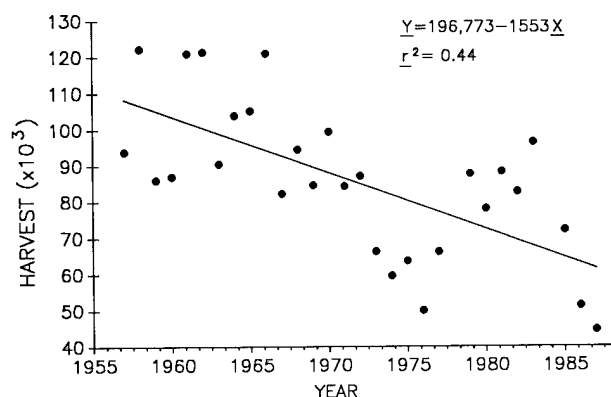


Fig. 10. Harvest of band-tailed pigeons in western Oregon, 1957–87.

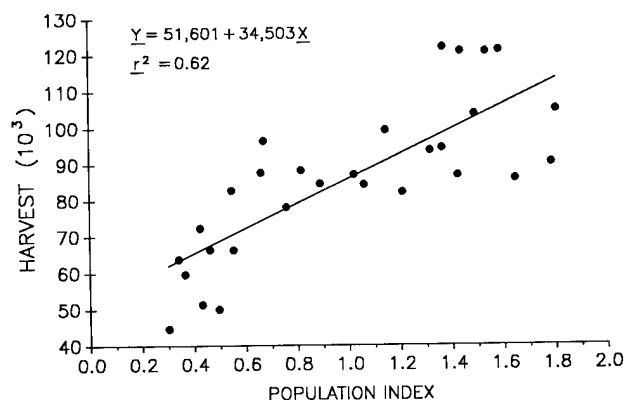


Fig. 11. Correlation of abundance of band-tailed pigeons and harvest in western Oregon, 1957–87.

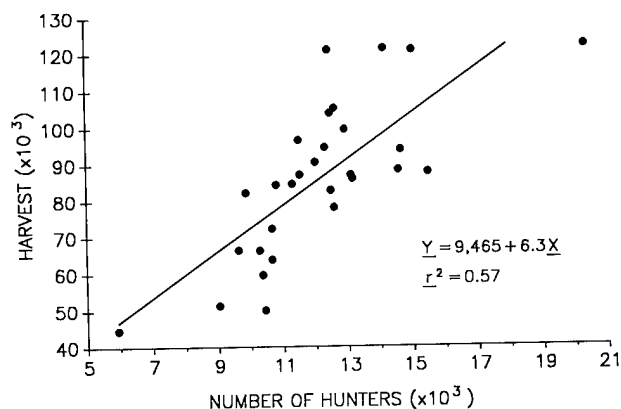


Fig. 12. Correlation of number of hunters and harvest of band-tailed pigeons in western Oregon, 1957–87.

Table 24. *Packets and wings received during a mail questionnaire survey of band-tailed pigeon hunters in Oregon, 1973–76.*

Year	N packets ^a containing wings	N wings	Wings per packet
1973	206	602	2.91
1974	284	862	3.03
1975	83	213	2.57
1976	284	714	2.51
Totals	857	2,391	2.79

^aEach packet represented the bag from 1 day of hunting by one hunter.

proportion of hunts resulting in a zero bag, and the number of hunters hunting each year. Thus, we considered the two estimates of reduced harvest to be consistent.

Analysis of the frequency distribution of number of band-tailed pigeons bagged per day revealed a similar pattern in all 4 years (Table 25). The number of hunts decreased exponentially as the number bagged per day increased up to the penultimate bag size. The frequency of the ultimate bag size (five or eight) was greater than the frequency of the penultimate bag size. Frequency distributions of birds bagged per day did not differ between 1973 and 1974 ($\chi^2 = 4.68$, $df = 7$, $P > 0.05$) when the bag limit was eight, nor between 1975 and 1976 ($\chi^2 = 3.55$, $df = 4$, $P > 0.05$) when the bag limit was five. When the frequency distribution was truncated at 5+ in 1973 and 1974, the combined distribution in those years did not differ ($\chi^2 = 2.93$, $df = 4$, $P > 0.05$) from the combined frequency distribution in 1975 and 1976. Thus, the reduction in harvest in 1975–76 resulted almost entirely from the reduced bag limit.

Spatial and temporal distribution of the harvest varied among the 4 years (spatial, $\chi^2 = 132.48$, $df = 15$, $P < 0.05$; temporal, $\chi^2 = 71.79$, $df = 15$, $P < 0.05$; Table 26; Table 27). We divided the state into six regions—roughly along the crest of the Coast Range Mountains and into thirds on a north–south basis—and the season into six, 5-day periods. Generally, more birds were bagged in coastal regions (64%) than in interior regions (36%), even though the interior regions were much larger (Table 26). Most of the harvest took place in the first 5 days of the season ($\bar{x} = 48.5\%$) and about 67.5% was in the first 10 days of the season (Table 27).

We examined the temporal and spatial distribution of harvest to assess what effect the change in bag limit, initiated in 1975, had on those distributions. Spatial distribution varied each year and we were unable to detect a pattern that might have been attributable to the reduced bag limit in 1975–76 (Table 26). However, temporal distribution of the harvest differed ($\chi^2 = 46.29$, $df = 5$, $P < 0.05$) between 1973–74 and 1975–76 (Table 27). In 1975–76, harvest was lower at the beginning of the season and higher during the middle of the season than in 1973–74. Possibly the reduced bag limit in 1975–76 reduced harvest early in the season, when the majority of the harvest took place, but some of the birds saved at the beginning of the season were harvested later in the season.

The average number of band-tailed pigeons bagged per day per hunter was highest in the first 5 days of the hunting season and declined thereafter, but the decrease was negligible in some years (Fig. 13). The rate of decline of average number of pigeons bagged as the season progressed was related directly to estimated total harvest; the greater the total harvest the more rapidly average bag size declined as the season progressed. Total harvest and changes in average number of birds bagged varied within relatively narrow limits during 1973–76. Nonetheless,

Table 25. *Frequency distribution of number of band-tailed pigeons bagged per day by hunters in western Oregon, 1973–76.^a*

Bag Size	Year							
	1973		1974		1975		1976	
	N	%	N	%	N	%	N	%
1	72	35.5	97	35.0	32	41.6	101	36.6
2	44	21.7	56	20.2	18	23.4	53	19.2
3	22	10.8	36	13.0	9	11.7	43	15.6
4	25	12.3	25	9.0	4	5.2	30	10.9
5	13	6.4	18	6.5	14	18.2	49	17.8
6	4	2.0	13	4.7				
7	6	3.0	6	2.2				
8	17	8.4	26	9.4				
Totals	203	100.0	277	100.0	77	100.1	276	100.1

^aDaily bag limit was reduced from eight in 1973–74 to five in 1975–76.

Table 26. *Spatial distribution (%) of band-tailed pigeons harvested by hunters in western Oregon, 1973-76.^a*

Regions	Year				Mean (N = 2,367)
	1973 (N = 588)	1974 (N = 861)	1975 (N = 210)	1976 (N = 708)	
North coast	20.2	16.5	9.1	15.5	16.5
Central coast	26.5	28.1	15.2	14.8	22.6
South coast	19.9	23.0	21.9	31.9	24.8
North interior	6.8	10.2	22.9	11.0	10.7
Central interior	15.7	12.8	24.3	14.6	15.0
South interior	10.9	9.4	6.7	12.2	10.4
Totals	100.0	100.0	100.1	100.0	100.0

^aBased on wings received from mail questionnaire survey.Table 27. *Temporal distribution of number of band-tailed pigeons harvested by hunters in western Oregon, 1973-76.^a*

Hunting season periods	Year					
	1973 N	1974 N	1973-74 %	1975 N	1976 N	1975-76 %
September						
1-5	325	435	52.5	88	300	42.3
6-10	120	152	18.8	44	133	19.3
11-15	65	115	12.4	41	103	15.7
16-20	33	46	5.5	16	93	11.9
21-25	27	76	7.1	17	53	7.6
26-30	18	37	3.8	4	26	3.3
Totals	588	861	100.1	210	708	100.0

^aBased on wings received in mail questionnaire survey.

this relation between total harvest and rate of decline in bag sizes indicated to us that hunting possibly reduced the size of the harvestable population, at least when the harvest exceeded 60,000 birds. However, this conclusion is tentative and needs to be tested with larger and more varied data sets.

Distribution of the harvest among three types of hunting locations (mineral sites, flyways, feeding area) varied among the 4 years ($\chi^2 = 45.7$, $df = 6$, $P < 0.05$; Table 28). Despite the significant difference, the overall pattern of harvest was relatively constant from 1973 to 1976. Slightly less than 40% of the band-tailed pigeons harvested were killed at mineral sites and slightly less than 20% at feeding areas.

Distribution of the harvest among hunting sites (by 5-day periods) was the same each year. At mineral sites, harvest was highest during the first half of the season and decreased to its lowest point at the end of the season (Table 29). At feeding areas the trend in harvest was the reverse of that at mineral sites; low at the beginning of the season and high near the end. The relative distribu-

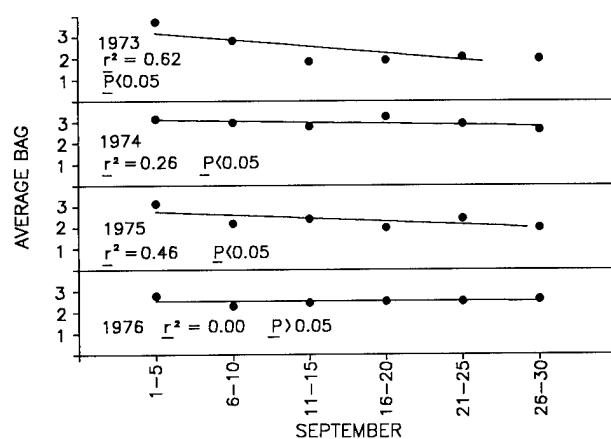


Fig. 13. Average number of band-tailed pigeons bagged per day per hunter during 5-day intervals of the hunting season in western Oregon, 1973-76.

Table 28. *Percent of band-tailed pigeons harvested at three types of hunting locations in western Oregon, 1973-76.^a*

Year	N	Percent of pigeons harvested			Totals
		Mineral site	Flyway	Feeding area	
1973	565	32.7	51.5	15.8	100.0
1974	824	41.0	40.7	18.3	100.0
1975	209	53.1	30.6	16.3	100.0
1976	708	34.5	43.7	21.8	100.0
Totals	2,306				
Weighted means		40.3	41.6	18.1	100.0

^aBased on wings received in mail questionnaire survey.Table 29. *Percent of band-tailed pigeons harvested at three types of hunting locations during six, 5-day periods of the hunting season in western Oregon, 1973-76.^a*

Period of hunting season	N	Harvest (%)			Total
		Mineral site	Flyway	Feeding area	
1-5 September	1,106	39.7	47.8	12.5	100.0
6-10 September	445	39.1	38.9	22.0	100.0
11-15 September	320	44.4	37.5	18.1	100.0
16-20 September	187	35.3	37.4	27.3	100.0
21-25 September	163	24.5	43.0	32.5	100.0
26-30 September	85	20.0	44.7	35.3	100.0
Totals	2,306				
Weighted means		38.1	43.3	18.6	100.0

^aBased on wings received in mail questionnaire survey.Table 30. *Mean number of band-tailed pigeons bagged per day by successful hunters at three types of hunting areas in western Oregon, 1973-76.^a*

Year	Mineral site		Flyway		Feeding area	
	N	\bar{X}	N	\bar{X}	N	\bar{X}
1973	53	3.49	95	3.06	43	2.07
1974	102	3.31	115	2.91	57	2.65
1975	31	3.58	32	2.00	17	2.00
1976	83	2.94	125	2.48	64	2.41
Totals	269		367		181	
Weighted means		3.27		2.72		2.36

^aBased on wings received in mail questionnaire survey.

tion of the harvest among the three types of hunting areas by 5-day periods was different each of the 4 years (1973, $\chi^2 = 38.3$; 1974, $\chi^2 = 47.6$; 1975, $\chi^2 = 69.0$; 1976, $\chi^2 = 93.4$; $df = 10$, $P < 0.05$, all years). We believed this pattern of distribution of harvest (fewer at mineral sites and more at feeding areas as the season progressed) reflected a real change in distribution of pigeons, but

also probably reflected a change in the distribution of pigeon hunters.

Hunters at mineral sites were more successful than hunters at feeding areas (Table 30). Although there was considerable annual variation, hunters at mineral sites bagged an average of 3.3 birds per hunter per day compared to 2.7 at flyways and 2.4 at feeding areas. The

Table 31. *Percent of band-tailed pigeons shot by hunters and not retrieved at three types of hunting locations in western Oregon, 1973-76.^a*

Year	Mineral sites		Flyways		Feeding areas		Total	
	N	% lost	N	% lost	N	% lost	N	% lost
1973	164	22.6	280	31.1	65	26.2	509	27.7
1974	365	18.4	393	23.7	183	28.4	941	22.5
1975	121	11.6	76	26.3	49	24.5	246	18.7
1976	299	19.7	362	18.5	196	22.0	847	19.7
Totals	949		1,111		483		2,543	
Weighted means		18.7		24.0		25.3		22.3

^aBased on wings received in mail questionnaire survey.Table 32. *Percent of juvenile band-tailed pigeons bagged by hunters at three types of hunting locations in western Oregon, 1973-76.^a*

Year	Mineral sites		Flyways		Feeding areas		Totals	
	N	Juv (%)	N	Juv (%)	N	Juv (%)	N	Juv (%)
1973	187	15.0	293	19.5	83	27.7	563	19.2
1974	336	11.0	328	15.9	147	23.8	811	15.3
1975	111	12.6	64	15.6	37	32.4	212	17.0
1976	249	9.6	332	19.6	147	23.1	728	16.9
Total	883		1,017		414		2,314	
Weighted means		13.2		18.1		25.1		16.9

^aBased on wings received in mail questionnaire survey.

change in allowable bag from eight to five in 1975, seemed to have little effect on hunter success at mineral sites and feeding areas. However, hunter success in flyways was lower (unpaired $t = 2.65$, $df = 367$, $P < 0.05$) in 1975-76 ($\bar{x} = 2.4$) than in 1973-74 ($\bar{x} = 2.9$).

During the 4-year survey about 22% of the band-tailed pigeons downed by hunters were reported as not retrieved (Table 31). Unretrieved harvest was higher at feeding areas ($\bar{x} = 25.3\%$, $\chi^2 = 8.46$, $df = 1$, $P < 0.05$) and flyways ($\bar{x} = 24.0\%$, $\chi^2 = 8.77$, $df = 1$, $P < 0.05$) than at mineral sites ($\bar{x} = 18.7\%$). Unretrieved kill was not different at flyways and feeding areas ($\chi^2 = 0.27$, $df = 1$, $P > 0.05$).

Unretrieved kill also was lower ($\chi^2 = 8.50$, $df = 1$, $P < 0.05$) during 1975-76 ($\bar{x} = 19.5\%$) when the bag limit was five than during 1973-74 ($\bar{x} = 24.3\%$) when the bag limit was eight. Possibly the reduced bag limit in 1975-76 encouraged hunters to select shots more carefully, thereby reducing the probability of shooting birds that could not be retrieved. To our knowledge reduced unretrieved kill (as a proportion of the retrieved kill) as a result of reduced bag limits has not been explored in other game birds.

Our overall estimate of 22% unretrieved kill probably was conservative because only successful hunters

responded to our survey and because hunters probably understated the number of birds they shot but did not retrieve. This estimate of unretrieved kill was substantial and similar to that reported for waterfowl (Craighead and Stockstad 1956; Martin and Carney 1977) and mourning doves (Nelson 1957; Haas 1977).

The proportion of the bag composed of juveniles varied by type of hunting location in the same pattern each of the 4 years of the survey (Table 32). Juveniles comprised the smallest proportion of the bag at mineral sites ($\bar{x} = 13.2\%$) and the largest proportion at feeding areas ($\bar{x} = 25.1\%$); differences among the three hunting locations were significant ($\chi^2 = 38.19$, $df = 2$, $P < 0.05$).

Discussion

Status

The fortunes of the band-tailed pigeon population breeding in Oregon has undergone several changes in the past 40 years. The population apparently experienced two periods of increase and two periods of decrease from 1950 through 1988. From 1950 through the mid-1960's,

the population index was variable and indicated a modest average rate of increase (2.4%). For the next 10 years (mid-1960's to mid-1970's) the population apparently declined precipitously (-10.4% per year). This decline was followed by a short period of increase extending into the early 1980's (7.1% per year). However, even at its highest point in the 1980's the population was still well below the long term average. The population subsequently began a second precipitous decline (-11.1% per year) and reached its lowest level since 1950 (30-35% of the long-term average). During the two periods of decline, the annual rates of declines were quite similar (-10.4% and -11.1%), but the annual rates of increase were dissimilar during the two periods when the population was increasing.

Historical information is too scanty to warrant speculation about potential causes of changes in the status of band-tailed pigeons during this period. Examination of the population dynamics of band-tailed pigeons should reveal relations between survival and recruitment that are relevant to assessing status. Most of our relevant data (survival, recruitment, age structure) were gathered during the 1960's and 1970's, a period when the band-tailed pigeon population was declining. Additionally, some of the important statistics were imprecise estimates of population parameters. Thus, the following analysis defines the range of performance of the population rather than providing an estimate of its exact performance. We approached the analysis by first estimating maximum potential production and then calculating necessary production and allowable survival under several scenarios.

Population Dynamics

Productivity

Band-tailed pigeon populations in Oregon seemingly had low recruitment into the fall population during the 1960's and 1970's, but a precise measurement of the recruitment rate was difficult to obtain. Our analysis indicated the fall population was composed of 15-30% young. Despite our imprecise estimate recruitment seemed to vary little from year to year. Lacking more precise data we suggest a recruitment rate of about 20-25% young.

Maximum potential recruitment was not high because band-tailed pigeons have a short nesting season and sin-

gle egg clutch. Most of the adult population began nesting in June and essentially completed it by mid-September. Each successful nesting required about 50 days, therefore, a maximum of two successful nestings could take place during the 100-110 day nesting period. Some adults apparently began nesting in late April (first young observed in June) and potentially could nest three times successfully. However, production from these adults was probably offset by adults that first began nesting in July and could nest successfully only once. Assuming that all adult pairs nested successfully twice and raised one young at each attempt, maximum potential recruitment would be one young per adult; this provides a fall population composed of 50% young. However, this estimate of biotic potential is inflated because SY adults apparently were much less productive than ASY adults and all nest attempts were not successful.

Based on rather sparse data on activity of crop glands, we estimated that SY band-tailed pigeons were only about one-third as productive as ASY adults. The low productivity of SY adults seems to be common in pigeons (Murton 1965; Lofts and Murton 1966). Lehrman and Wortis (1967) demonstrated in controlled experiments with ringed turtle-doves (*Streptopelia risoria*) that both age and breeding experience affected production of young. Experienced doves were more successful at raising young than inexperienced doves of the same age, and "...all of the demonstrable improvement occurred between the first and second breeding experience."

SY band-tailed pigeons composed about 11-21% of the breeding population in spring. Assuming they were one-third as successful as adults, they potentially fledged 0.66 young per pair. Thus, if the breeding population was composed of 16% SY (median figure) and 84% ASY adults, then maximum potential recruitment of young would be about 47% young (Table 33). In this simplified analysis we assumed zero mortality between initiation of nesting and recruitment of young (an assumption of equal mortality of ASY and SY birds, and no young recruited by breeding birds that died during the summer, produced the same proportion of the three age classes in the fall population).

The proportion of juveniles in the fall population in the biotic potential model (47%) was about 50% greater than the rate we estimated (20-25%) in the real population.

Table 33. *Biotic potential of a hypothetical population of 100 band-tailed pigeons.*

	ASY Adult	SY Adult	Juvenile	Totals
Number in breeding population	84.0	16.00		100.0
Young per adult	1.0	0.33		
Potential production	84.0	5.30		89.3
Number in fall population	84.0	16.00	89.3	189.3
Percent in fall population	44.4	8.40	47.2	100.0

However, assuming a 40% nest success rate (equal for ASY and SY breeders) yielded 26.3% juveniles in the fall population, 61.9% ASY and 11.8% SY band-tailed pigeons (Table 34). Our median estimate of age structure in the fall population was 23% juvenile, 12% SY, and 65% ASY.

Although we have no data on nest success, a nest success rate of 40% seems reasonable for band-tailed pigeons. MacGregor and Smith (1955) reported 53% nest success in California. Most of the nests they studied were active when discovered; calculation of success from such nests overestimates actual rates of nest success because nests destroyed prior to discovery are not included in the sample (Mayfield 1961, 1975; Miller and Johnson 1978).

We suggest the apparent low productivity of band-tailed pigeons in Oregon was that which could be expected from the population, given the phenology of food plants and time available for nesting. Thus, changes in population abundance would not seem to be caused solely by reproduction failure. Rather, the population seems to be producing as many young as could be expected and this rate of productivity seems not to vary annually.

Population Status

We used the structural models of Henny et al. (1970) to calculate necessary production and survival to maintain a stationary population. To use these models we first had to calculate age specific recruitment and survival schedules.

We calculated mean annual survival of 63.7% (1965–72) for adults (Table 21). This estimate was based on combined SY and ASY birds, presumably in approximate proportion to their appearance in the population. We have no evidence that survival of the two age classes differed, and thus assumed 63.7% survival for both. Insufficient numbers of juvenile band-tailed pigeons were banded to calculate survival rates directly.

We estimated juvenile survival based on age structure of the fall population and mortality rate of adults. Assuming an age structure of 23% juveniles, 12% SY, and 65% ASY adults in the fall; equal survival rates of SY and ASY birds; and constant recruitment and popula-

tion size; the juvenile survival rate was about 52% (0.12/0.23). For a population declining at an annual rate of 10.4%, survival of juveniles would be 47%. This estimate is similar to that calculated by Silovsky (1969; 49.2%), but less than those calculated by Braun et al. (1975; 58.3%) and Kautz and Braun (1981; 66%) for band-tailed pigeons in the southern Rocky Mountains.

To calculate age specific recruitment we used the fall age structure and partitioned the 23% juveniles among the 65% ASY and 12% SY adults (Table 35). Because SY birds were only one-third as productive as ASY adults, they produced 5.8% of the juveniles or 0.11 young per SY adult. ASY Adults produced 94.2% of the juveniles at a rate of 0.33 juveniles per ASY adult.

By use of the special case I of Henny et al. (1970; breeding first takes place at the end of the 1st year of life), average recruitment would be 0.69 young per AHY adult to maintain a stable population with ASY and SY survival of 0.637 and juvenile survival of 0.522. The age structure we observed indicated average recruitment of 0.30 young per adult (Table 35). This analysis indicated that recruitment was only about 40% of that necessary to maintain population stability. However, 0.69 young per adult implies production near the estimated maximum potential (0.89 young per adult; Table 33) of band-tailed pigeons in western Oregon.

A recruitment rate of 0.69 juveniles per adult results in a fall age structure of 40.8% juveniles, 9.5% SY, and 49.7% ASY adults, assuming that breeders occurred in the ratio we observed (0.19 SY:1 ASY). This age structure indicates that juveniles had a survival rate of 23.3% (9.5/40.8). The 40.8% juveniles in the fall population is much greater than the maximum proportion of juveniles we ever observed (30% at mineral site A). Conversely, assuming juveniles had a survival rate of 0.522, the rate we calculated, the fall age structure would be 40.8% juveniles, 21.3% SY, and 37.9% ASY adults. Productivity would be 0.91 juveniles per ASY adult and 0.30 juveniles per SY adult to produce a mean recruitment of 0.69 juveniles per adult. These age-specific rates are nearly the same as the rates used to calculate maximum reproduction potential (Table 33) and hence, do not seem to be realistic. From this analysis we concluded the population was not capable of adjusting reproduction to match the estimated survival rates.

Table 34. *Potential production of young by a hypothetical population of 100 band-tailed pigeons, assuming a nest success rate of 0.40.*

	ASY Adult	SY Adult	Juvenile	Total
Number in breeding population	84.0	16.0		100.0
Production of fledged young	33.6	2.1		35.7
Number in fall population	84.0	16.0	35.7	135.7
Percent in fall population	61.9	11.8	26.3	100.0

Table 35. *Procedure for partitioning recruitment of juveniles among SY and ASY band-tailed pigeons and calculation of age-specific productivity.*

Item	ASY Adults	SY Adults	Totals
a. Percent in fall population	65.0	12.0	77.0
b. Relative contribution to productivity per individual	1.00	0.33	0.90
c. Relative contribution of age class ($a \times b$)	65.0	4.0	69.0
d. Percent contribution of age class to productivity ($c/\Sigma c$)	94.2	5.8	100.0
e. Productivity of age class ($d \times 23$)	21.7	1.3	23.0
f. Productivity per individual (e/a)	0.334	0.11	0.299

Population stability also can be maintained by holding recruitment at the estimated rates and adjusting survival; Henny et al. (1970) provided a procedure for calculating allowable mortality. Assuming recruitment rates of 0.111 for SY and 0.334 for ASY adults, survival was calculated to be 0.679 for juveniles and 0.829 for adults (SY and ASY) to maintain a constant population size. In a stable population the 23% juveniles would result in 15.6% SY adults when subjected to a survival rate of 0.679; ASY adults would compose 61.4% of the population. This age structure is similar to the age structure we observed (12% SY and 65% ASY adults). This solution to the allowable mortality formula sets survival of SY birds (s_1) equal to survival of ASY birds (s_2) and both are proportional to survival of juveniles (s_0). Thus, $0.637:0.522 = 0.829:0.679$. Henny et al. (1970) provided an alternate solution which sets s_x at the survival rate (0.637) estimated from banding data and calculates juvenile survival necessary to maintain a stable population with the estimated age-specific recruitment rates. This solution produced a calculated juvenile survival of 1.44, an obviously unrealistic survival rate. Hence, only the first solution provided a usable answer to the question of allowable mortality. From that solution, we conclude that survival of both adults and juveniles was insufficient to maintain population stability. With the estimated schedule of recruitment (0.111 juvenile per SY adult, 0.334 juveniles per ASY adult), survival would need to be 1.3 times greater than current estimates ($0.829/0.637$; $0.679/0.522$) to prevent the population from decreasing.

The structural model of allowable mortality produced survival rates that were high (adults = 0.83, juveniles = 0.68) but not unreasonable and that were consistent with the observed age structure. These survival rates also were consistent with survival rates observed in Colorado (adults = 0.73, juveniles = 0.66; Kautz and Braun 1981). From these analyses we conclude that the population decline from the mid-1960's to the mid-1970's resulted principally from excessive mortality; insufficient

recruitment of young probably had at most only a minor role in the decline of the population.

According to the analysis of the population index, the population was increasing modestly prior to the mid-1960's and after the mid-1970's. Unfortunately, we lack data with which to estimate recruitment and survival schedules during those periods, and hence, were unable to contrast those variables during increasing and decreasing population trends. Collection of data on survival and recruitment in the future would provide valuable insights into the population dynamics of band-tailed pigeons.

Effects of Hunting

If inadequate survival was the primary cause of population decline in Oregon from the mid-1960's to the mid-1970's, the role of hunting mortality as a contributor to that decline requires examination. Although we lack data (kill rates, hunting mortality) necessary for a direct quantitative evaluation of the role of hunting, we can examine, at least qualitatively, the effect of hunting on the population.

In 1975, hunting regulations in Oregon, Washington and California were made more restrictive, the harvest of pigeons decreased, and the population index increased. However, hunting regulations became even more restrictive in the late 1980's, yet the population index decreased, and the harvest also apparently decreased. Thus, restrictive hunting regulations were associated with both an increase and a decrease in the population index, and provide no insight into the effect of hunting on band-tailed pigeon populations. Hunting restrictions only indirectly affect harvest rates, and it is the harvest rate that potentially influences survival.

To examine the relation between harvest rates and population trend, we derived a relative index to the kill rate by dividing estimated harvest by the population index (Fig. 14). The kill rate index was significantly ($P < 0.05$) lower during 1957–65 ($\bar{x} = 291,000$), a period of increas-

ing abundance of band-tailed pigeons, than during 1966–75 (\bar{x} = 592,000), a period of decreasing abundance. However, the kill rate index during 1976–83 (\bar{x} = 468,000), a period of increasing abundance, was not different from those of either of the two previous periods.

Because of the coarseness of the data, both of these analyses would likely only detect a strong and direct relation between hunting and population abundance; subtle and indirect effects of hunting would not be detectable. Further, harvest of band-tailed pigeons fluctuates greatly which would obscure relations based on average values.

Band-tailed pigeons are occasionally subjected to large harvests, mostly in California. Historically, a huge harvest was reported in central California in the winter of 1911–12 (Grinnell 1913; Neff 1947). This incident, involving both sport and market hunters, prompted concern among conservationists about the survival of the band-tailed pigeon population and resulted in Congressional action that outlawed hunting of band-tailed pigeons from 1913 to 1932. Einarson, in an unpublished report (Oregon Cooperative Wildlife Research Unit, Corvallis) associated the scarcity of band-tailed pigeons in Oregon in 1950 to a large harvest in California the previous year. The largest measured harvest took place in 1972 when over 724,000 band-tailed pigeons were taken, 534,000 in California alone (Table 23). The population index in Oregon was more than halved between 1972 and 1973 (Fig. 9). Large harvests also were reported in 1962, 1966, and 1968. The large harvests are seemingly associated with abundant mast crops at low elevations in central California; areas that are easily accessible to large numbers of hunters (Neff 1947). These occasional heavy kills probably represent catastrophic losses to the band-tailed pigeon population, losses that may influence the population for many years. Such catastrophic losses may play a major role in the population dynamics of band-tailed pigeons but current data are unsuitable for modeling these episodic events and their consequences for the population.

Any attempt to assess the effects of hunting mortality on band-tailed pigeon populations must be able to incorporate the episodic losses that seemingly occur at long and unpredictable intervals. With the currently available data, the question of the effect of hunting on band-tailed pigeons is unresolved. The answer has important management implications and the question needs to be resolved.

Effects of Hunting at Mineral Sites

Hunting at mineral sites may have a greater effect on band-tailed pigeon populations than number of birds harvested would indicate. Although only about 20% of the hunts took place at mineral sites, nearly 40% of the harvest of band-tailed pigeons took place there (Table 28). These figures were minimum estimates because an unknown proportion of hunts reported as taking place in flyways probably took place in the vicinity of mineral sites. Hunters at mineral sites were most successful (average bag = 3.3 per day, Table 30). However, the lowest proportion of juveniles was bagged at mineral sites (\bar{x} = 13.2%; Table 32); a proportion much lower than estimated for juveniles in the population (23%). Observation at one mineral site in early September revealed an average of 20.4% juveniles among band-tailed pigeons visiting the site but only 8.4% of the band-tailed pigeons bagged at this site were juveniles. Adults were seemingly more vulnerable to hunting at mineral sites than juveniles. The behavior of band-tailed pigeons at mineral sites, whereby they attempted repeatedly to approach and land near the mineral deposit despite activities of hunters, probably increased the vulnerability of adults. Juveniles, because they rarely consumed minerals, may be less persistent than adults at returning to mineral sites when hunters are present.

Mineral sites are important to band-tailed pigeons and consumption of minerals may be an essential supplement to the diet of nesting adults. Fledging reaches a

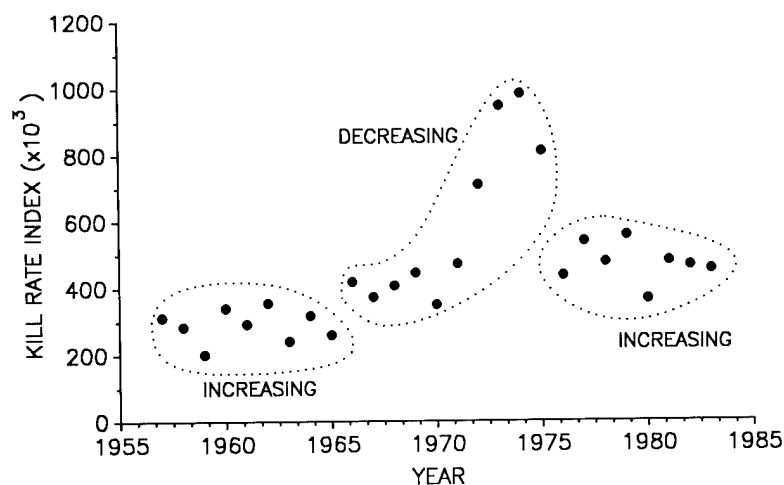


Fig. 14. Kill rate index for band-tailed pigeons in western Oregon during periods of increasing and decreasing abundance, 1957–83.

peak in late August—early September; hunting seasons in Oregon, as well as Washington and British Columbia, traditionally opened on 1 September. Because many adults are still nesting in early September, they are the pigeons visiting mineral sites and most likely to be shot by hunters. Of band-tailed pigeons harvested at the one mineral site where we observed hunting, 77% ($N = 38$) had active crop glands, which indicates they were still nesting. These birds were experienced breeders or were SY adults about to complete their reproduction apprenticeship. In either event they were a valuable component of the population, and from the standpoint of resiliency of the population to exploitation, the least expendable component. Hunting at mineral sites directed the harvest at experienced breeders and may reduce the ability of the population to compensate for hunting mortality by increased reproduction. Additionally, birds harvested in early September seemingly were local residents. Thus, hunting at mineral sites directed the harvest at experienced breeders of resident subunits of the population.

Reproduction Ecology

Food

Availability of food may strongly influence reproduction of band-tailed pigeons, especially in regard to timing of initiation of nesting. When band-tailed pigeons first arrived in Oregon in spring they consumed a variety of food items, and were attracted easily to baited trap sites; both behaviors were indicators of food scarcity. In early to mid-June, the pigeons began consuming berries of Pacific red elder almost exclusively as it became available, and the birds deserted baited trap sites. Their diet during the rest of the summer remained berries, and they consumed relatively few species of berries, (cascara buckthorn and two types of elder). Casual observations indicated these berries were abundant after mid-June.

The first appearance of substantial numbers of young at mineral sites in Oregon was in late July and early August. Some band-tailed pigeons began nesting as early as April but, judging from fledging phenology, most young were produced from late July to mid-September. Thus, a relation between food abundance and nesting activity of band-tailed pigeons in Oregon seemed quite clear to us.

In British Columbia, reproduction activity of band-tailed pigeons coincided with the consumption of berries (March and Sadleir 1970, 1972), and the chronology of reproduction was nearly identical in British Columbia and Oregon. Gutierrez et al. (1975) noted a direct relation between food abundance and reproduction of band-tailed pigeons in Colorado and New Mexico, including nesting in fall in New Mexico, apparently in response to a locally abundant acorn (*Quercus* spp.) crop. They

concluded that food was a proximate factor in stimulating reproduction.

Band-tailed pigeons breed and nest over a much longer period in California than in Oregon. MacGregor and Smith (1955) reported nesting from February through October in central California. They made no attempt to relate food to nesting activity in California but Smith (1968) reported that band-tailed pigeons fed extensively on grain from February to July and on mast and berries from September to December.

Murton (1965) demonstrated a relation between nesting activity of wood pigeons (*Columba palumbus*) in England and availability of cereal grains. About 75% of the fledged young hatched during July and August when adults were feeding almost exclusively on grains. Young hatching before July, when adults fed mostly on greens because of the scarcity of grain, had lower fledging rates (38%) than young hatching in July and August (82%). Murton (1965) concluded that abundance of food regulated initiation of nesting and those adults attempting to nest when food was not abundant were largely unsuccessful.

In wood pigeons, abundance of food and initiation of nesting was apparently interconnected via a behavioral mechanism. Males began establishing territories as early as February even though food was not abundant in February. However, males were unable to spend much time in their territories because of the time-consuming requirements of foraging (Murton 1965; Lofts and Murton 1966; Lofts et al. 1966). As food supplies increased, pairing took place. When food became abundant the pair remained in the territory for extensive periods each day; courtship, nest construction, and egg laying took place then.

Stimulation of sexual activity of the female by the male has a physiological basis (Hinde 1965; Lehrman 1965; Lofts and Murton 1973). Courtship behavior by a male bird induces growth of the ovaries and oviduct, and an interest in nest construction by the female. Nest building activity then leads to ovulation. Courtship and nest building apparently serve as stimuli for the release of hormones (gonadatrophins, estrogen and progesterone) that effect physiological and behavioral changes. In some species (e.g., canaries, *Serinus canaria*) courtship by the male serves to initiate the chain of events (enlargement of ovary and oviduct, nest construction, egg laying, incubation) but his presence after initial courtship is not essential (Hinde 1965). In pigeons and doves, the continued presence of the male is necessary for production of eggs (Lehrman 1965). Males gather the material that female doves and pigeons use to construct the nest (Lehrman 1965; Peeters 1962), and courtship and involvement in nest construction by both sexes may be necessary for ovulation to take place. However, courtship alone (mates were separated by a partition) stimulated ovula-

tion in rock doves (*Columba livia*; Matthews 1939) and ringed doves (Lehrman 1964). Thus, the behavior of the male, stimulated by photoperiod, regulates sexual activity leading to egg laying by the female.

Gonadal enlargement in males takes place before gonadal enlargement in females. Males may be responding to photoperiods but in band-tailed pigeons even relatively short photoperiods (10 h light: 14 h dark) stimulated growth of testes (Gutierrez et al. 1975). The apparent ease with which males become sexually active would insure that when food becomes abundant, reproduction could begin without undue delay, but the need for the female to be sexually stimulated (5–7 days in ringed doves; Lehrman 1965) by the male in a territory would delay reproduction long enough to insure that a sufficient food source was present to provide a high probability of successfully raising young.

We believe the chain of events described above regulates nesting phenology of band-tailed pigeons. Such a sequence would explain the predictable chronology but short nesting season and consistent production of young we observed in Oregon and the long, but variable nesting season and production of young observed in California and New Mexico. The strong seasonality and consistent, abundant berry production in the Northwest results in a short but consistently timed nesting season. In California and New Mexico, seasonality is weaker and results in long nesting seasons. However, abundant food supplies, especially acorns, are less predictable in the south, hence, reproduction effort varies annually and even locally.

Use of Minerals

Attraction and concentration of band-tailed pigeons at mineral sites has been reported throughout their range in North America (Packard 1946; Morse 1957; Smith 1968; Fitzhugh 1970; March and Sadleir 1972). In coastal regions, band-tailed pigeons frequently and consistently gather at mineral sites in Oregon, Washington, and British Columbia. However, in California mineral sites are less common and band-tailed pigeons consistently gather at only a few sites. In the southern Rocky Mountain region, use of mineral sites by band-tailed pigeons is inconsistent (Fitzhugh 1970).

Although band-tailed pigeons spend a small proportion of their time consuming minerals while at such sites, the presence of a mineral deposit seems to be the principal attractant. Several authors (Einarsen 1953; Morse 1957; Smith 1968) suggested that the pigeons were attracted to mineral sites principally during fall migration. However, use of minerals coincided with nesting in our study. Consumption of mineral began in early to mid-June, with increasing numbers of band-tailed pigeons at mineral sites until late August–early September. The appearance of band-tailed pigeons at mineral sites was negligible by late September. Nesting followed nearly

the same phenology: initiated in mid-June, fledging peaked in late August, and was completed by mid- to late September. March and Sadleir (1970, 1972) also noted a close correlation between reproduction activity and use of minerals and thought this relation was functional and not merely coincidental.

The high rate of homing to mineral sites and high fidelity of individual band-tailed pigeons for specific mineral sites indicated that accessible mineral deposits were an essential resource. These traits would develop and persist only if access to a concentrated mineral deposit provided a selective advantage and then only if those deposits were relatively scarce. About 125 mineral deposits used by band-tailed pigeons have been identified in western Oregon; western Oregon contains about 250,000 km². This density (one per 3,000 km²) indicates mineral sites are a relatively scarce resource. Also, band-tailed pigeons readily discovered and used newly revealed deposits. One of our intensively studied sites was a mineral deposit exposed during construction of a levee; another resulted from a gas exploration well that tapped an underground reservoir of mineralized water. Thus, mineral deposits seem to be a key resource for band-tailed pigeons during the breeding season and may be more important than food or nesting sites in determining distribution of the birds during the nesting season. March and Sadleir (1975) investigated calcium distribution in band-tailed pigeons in British Columbia and reported that serum calcium was highest in the females during ovulation and in both sexes during the phase of active crop milk production. Females apparently used calcium stored in medullary bone during ovulation and during formation of crop milk; medullary bone was present until the end of the nesting cycle. However, males lack medullary bone, and femur calcium did not change during the nesting cycle, although serum calcium levels were elevated during the phase of active crop milk formation. March and Sadleir (1975) suggested that in males, blood possibly acted as a storage depot for calcium when crop milk was forming.

Crop milk contains a high concentration of calcium (5 mg/g) and, when feeding young, adults must obtain about 10 mg of calcium per day to maintain calcium balance (March and Sadleir 1975). March and Sadleir (1975) concluded that consumption of minerals was necessary to satisfy the high calcium demands of reproducing band-tailed pigeons. They also reported that females used mineral sites more extensively than males during the nesting season, except at the end of the nesting season, and speculated that females had higher calcium requirements (production of eggs) than males. However, that conclusion was based on sex ratios derived from apparently biased samples.

March and Sadleir (1975) reported a preponderance of females at mineral sites in British Columbia from May to August, (the female to male ratio varying from 5.8 to

2:1), but a preponderance of males in September (0.6:1). However, we believe their sample was biased because they collected birds "...between 10 a.m. and 12 noon" (March and McKeown 1973) but "...large samples were obtained from cooperating hunters at the beginning of September each year" (March and Sadleir 1972). Because females predominated in the late morning period at mineral sites, samples collected during that period would be expected to contain mostly females.

Our observations at mineral sites revealed an even sex ratio of band-tailed pigeons from daylight to 1200 h from June to August, but more males than females in September (0.2:1), similar to that (0.6:1) reported by March and Sadleir (1975). We believe the even sex ratios we observed at mineral sites in Oregon was a correct assessment of the use of minerals by males and females. An even sex ratio would suggest that males and females had about equal mineral requirements. Because males required additional calcium only when the crop gland was active, formation of crop milk was probably the primary calcium demand that resulted in consumption of minerals.

In September, as the end of the nesting season approached, the numbers of band-tailed pigeons using mineral sites declined. Among the band-tailed pigeons continuing to visit mineral sites, there was a preponderance of males. Female rock doves frequently cease feeding the nestling before it is fledged, leaving the male to finish caring for the young (Whitman 1919). Possibly male band-tailed pigeons continued to require supplemental calcium later in the nesting season than females. Also, females could deplete calcium from medullary bone while feeding their last young of the season because medullary bone persists until crop gland activity is completed (March and Sadleir 1975). Thus, the reason females terminated consumption of minerals earlier than males probably resulted from females retiring from brooding responsibilities earlier and because they obtained calcium from resorption of medullary bone.

Relation of Minerals to Diet

Many species of pigeons and doves consume minerals, but it is by no means a universal trait of columbids, nor is it a universal trait among band-tailed pigeons. According to Goodwin (1970), the most notable group of pigeons that consume minerals are the fruit pigeons (*Ducula* spp.); as their name implies the diet of these birds is almost exclusively fruits or berries. Mineral consumption has also been reported for some species of green pigeons (*Treron* spp.) and typical pigeons (*Columba* spp.).

We believe that consumption of minerals by band-tailed pigeons is related to their berry diet in Oregon. Berries of all kinds tend to have low mineral content, especially in calcium. We tested two samples of berries; blue elder (*Sambucus cerula*) berries contained 0.12%

calcium and Pacific red elder berries 0.06% calcium (measured on a dry weight basis). A mineral supplement is routinely recommended for breeding flocks of rock doves, but specific mineral requirements have not been determined (Levi 1969). Assuming band-tailed pigeons have similar requirements to rock doves, elder berries provided a diet deficient in minerals, especially calcium. However, elder berries have a high energy content (6.75 kcal/g; March and Sadleir 1975) and adequate protein (12.2% dry weight), and are therefore a good food for nesting band-tailed pigeons.

Mourning doves probably have mineral requirements similar to those of band-tailed pigeons because both have small but repeat clutches and both feed crop milk to their young. We frequently observed mourning doves (2–10 individuals per day) at two of the three mineral sites we studied intensively, yet we did not observe them consuming minerals. Judging from courtship activity and presence of recently fledged young, at least some of these doves were nesting. However, doves feed on seeds rather than on berries. Adequate mineral was probably obtained from seeds and from foraging on the ground. Hence, doves may not require a mineral supplement while nesting.

In California, consumption of minerals by band-tailed pigeons is infrequent but their diet is variable, consisting of agricultural crops as well as native seeds, buds, and fruits (Smith 1968). In the southern Rocky Mountains band-tailed pigeons infrequently use mineral sites but feed extensively on cereal grain in cultivated fields (Braun 1976).

We hypothesize that in the Northwest, berries (principally Pacific red elder) provided the energy source necessary for nesting. As a result of dependence on berries, band-tailed pigeons must seek a mineral supplement to their diet. The most likely chemical element sought is calcium and it is most likely involved in production of crop milk, by both sexes, and for production of eggs and eggshells by the female. We suggest that mineral deposits consequently are an essential resource to band-tailed pigeons for successful reproduction and as a result they home strongly to mineral sites.

Research Needs

The research needs for band-tailed pigeons are many and varied. Our analyses were hindered in many cases by lack of information with which to test assumptions and hypotheses. For instance, our analyses of population biology contained many assumptions that constrained the outcome to sketching the boundaries within which population performance probably lies. In particular, the juvenile component of the population is particularly not well known.

Estimates of both recruitment and survival of juveniles are imprecise. They were calculated from indirect sources of information that required many untested assumptions. Information on productivity derived directly from pairs and nests is needed. Recent advances in miniaturization of telemetry transmitters provides a means for directly acquiring data from which recruitment can be estimated. The ability to monitor pairs during the nesting season would also yield valuable information on nesting habitat, nesting biology, and survival of pairs during the summer.

Survival of juvenile band-tailed pigeons was recognized as an important need by Jeffrey et al. (1977), but estimates of survival have not been achieved. The current restrictive hunting regulations yield small sample sizes that preclude band recovery analysis as a method of estimating survival rates of both adults and juveniles. Even when hunting regulations were liberal, low band recovery rates yielded small sample sizes. Juveniles have never been banded in sufficient numbers in the Pacific population to yield useful band recovery data. Simultaneous estimates of survival rates of juveniles and adults (also perhaps SY band-tailed pigeons) are necessary for population modeling. Estimates of survival need to be of sufficient resolution to assess the effects of the large hunting losses that periodically take place. Those losses may have multi-year consequences, yet compensatory responses may also occur. Management programs that disregard these large episodic losses may be undone by them.

Radiotelemetry methods provide a means of intensively monitoring a small sample of birds from which survival rates can be estimated. Telemetry would allow estimates of survival functions annually, as well as during specific time intervals; for example, nesting season, migration, hunting season. Frequent relocation using aircraft will be more costly but necessary and more efficient to track the highly mobile and migratory band-tailed pigeon. Information on timing and phenology of migration, especially fall migration, would also be generated by the telemetry methodology, thereby increasing the outputs from the research. Current presumptions about fall migration affect management actions; for example, timing of hunting seasons. The question of when band-tailed pigeons begin fall migration needs to be answered.

Surprisingly little is known about the habitat needs of band-tailed pigeons and about the habitats they utilize. Forest environments in the Northwest have undergone major changes in the past century and the suitability of current forests for band-tailed pigeons is little known; so little that even speculation is futile. Even basic information on nesting sites in the Northwest is lacking. Until specific and quantitative information on habitat needs of band-tailed pigeons is available, management efforts cannot be fully effective. Once again, telemetry could

be employed to successfully study habitat use by band-tailed pigeons.

Telemetry is an enticing methodology that potentially should provide information about band-tailed pigeons that has previously been unobtainable. However, we recommend that telemetry be carefully and judiciously undertaken to avoid generating flawed results. Methods of attaching transmitters to band-tailed pigeons needs to be thoroughly investigated with captive birds or surrogates (e.g., rock doves) before field studies are initiated.

While there often are compelling reasons to undertake research that promises to fulfill the immediate needs of management, research efforts that do only that are likely to be less than fully fruitful. That is, gathering data to estimate specific parameters may fulfill an immediate need, but such a focus may not have much enduring value. An effort must be made to understand the mechanisms that cause parameters to take on their estimated values.

Summary

Adult band-tailed pigeons congregated at mineral sites from June to September; peak numbers occurred in mid- to late August. Typically, males arrived shortly after dawn and departed in mid-morning; females arrived in mid-morning and departed in mid-day. Sex ratios were approximately 1:1 during most of the summer, but males greatly outnumbered females in September. Appearance of band-tailed pigeons at mineral sites corresponded with nesting.

Analysis of 4 sets of data (crop gland activity, specific reproduction events, age distribution of juveniles shot in September, and proportion of juveniles at mineral sites) indicated fledging of young began in June, peaked in mid- to late August and continued into mid- to late September. SY band-tailed pigeons were only about one-third as productive as ASY adults.

From June through September, band-tailed pigeons fed mostly on berries of Pacific red elder, blue elder and cascara buckthorn. The availability and consumption of these berries coincided with nesting. Before June and the ripening of Pacific red elder, widespread movement in search of food was clearly a major activity and suggests that food may have been relatively scarce before June.

Band-tailed pigeons homed very strongly to mineral sites, using one or several adjacent sites during a year and in subsequent years. Females returned at higher rates than males to the same mineral site in subsequent years, although the data base was too small to assess the relevance of the difference. Band recoveries indicated that band-tailed pigeons were resident in Oregon from at least April through September and that most returned to the same local area throughout their life.

Autumn migration in Oregon is commonly believed to begin in August and to be completed by mid-September. However, in a spatio-temporal analysis of band recoveries from the Northwest, we were unable to detect migratory movements in September. We think the previous reports of early migration were based on inconclusive observations and were incorrect.

Based on hunter shot samples, recruitment of young seemingly varied little annually. From 15 to 18% of the harvest was composed of juvenile band-tailed pigeons in 1973–76; these values compared with 16.5 to 18.6% reported in 1966–67. Proportion of juveniles present at mineral sites in late August varied from 7 to 25%. We suggest that actual recruitment was between 15–18 and 25–30% but are unsatisfied with our inability to explain much of the variation in our data.

From 9 to 17% of the adult band-tailed pigeons trapped in spring were SY (1st calendar year after hatching) birds. SY band-tailed pigeons composed 14% of the adults trapped at mineral sites, and 12% of the band-tailed pigeons collected during summer. We calculated that the breeding population in spring was composed of about 15% SY and 85% ASY (after second year, 1+ years old) adults. The fall population consisted of 23% HY (hatching year), 12% SY and 65% ASY band-tailed pigeons.

Survival of adult (AHY, after hatching year) band-tailed pigeons from 1965 to 1973 was year specific, varying from 44.5 to 85.3% and averaging 63.7%. Although we observed distress in some birds upon release after banding, first year recovery rates were not different from those during subsequent years.

An index to population size based on annual counts of band-tailed pigeons at eight mineral sites in western Oregon increased at an average annual rate of 2.4% from 1950 to 1965 and 7.1% from 1975 to 1984. The index decreased at annual rates of 10.4% from 1963 to 1978 and 11.1% from 1980 to 1988.

From 1957 to 1987 harvest of band-tailed pigeons in Oregon varied from 45,000 to 122,000 and represented about 22% of the total harvest in Oregon, Washington and California. The Oregon population index was related to harvest in Oregon ($r^2 = 0.62$), but was poorly correlated with total harvest and to the harvest in Washington and California (r^2 's of 0.24 to 0.30).

Average daily bag was lower in 1975–76 (2.53) when the bag limit was five than in 1973–74 (2.97) when the bag limit was eight. The harvest in Oregon also declined from 63,000 per year in 1973–74 to 56,900 in 1975–76. The reduction in bag limit from eight to five produced a 10–14% reduction in harvest.

Harvest was concentrated during the early part of the 30 day season; 48.5% in the first 5 days and 67.5% in the first 10 days. About 40% of the harvest took place at mineral sites, about 20% at feeding areas, and the remain-

der along flyways. At mineral sites, harvest was highest early in the season and the proportion of the bag that was juveniles was low (13.2%). At feeding areas, harvest was highest at the end of the hunting season and the proportion of juveniles was high (25.1%).

Simplified models based on average values for age structure, survival rates, and recruitment rates indicated: (1) production at the maximum biotic potential would produced a fall population containing about 47% young, (2) necessary production to maintain a stable population size given the estimated age structure and survival rates (63.7% for AHY and 55.2% for HY) produced a population with 40.8% young; (3) necessary survival to maintain a stable population size given the estimated age structure and age specific productivity (0.11 for SY and 0.33 for ASY adults) was 0.679 for juveniles and 0.829 for SY and ASY adults, and produced a fall population of 23% HY, 15.6% SY and 61.4% ASY. Only the results of the latter simulation were considered realistic and indicated that the survival rates estimated for the actual population (HY = 55.2%, and SY and ASY = 63.7%) were inadequate to maintain population size.

Effect of hunting on population was indeterminable. Restrictive hunting regulations and low to moderate values of a kill rate index were associated with both a period of increasing and a period of decreasing abundance of band-tailed pigeons. However, hunting at mineral sites in early September may disproportionately harvest experienced breeding adults, the most productive portion of the population.

Band-tailed pigeons are periodically subject to large harvests associated with large acorn crops in areas readily accessible to large numbers of hunters in California. These catastrophic losses take place irregularly, but may have a major influence on population trends for many years.

Food abundance, rather than photoperiod, seems to be a primary regulator of reproduction activity in band-tailed pigeons. Males are reproductively stimulated by a short photoperiod (10 h) but females are stimulated behaviorally by the male. When food is abundant, males have sufficient time to stimulate females, resulting in nest building and ovulation. Thus, nesting begins only when food is abundant enough to insure a high probability of successfully raising young.

Large amounts of calcium are needed to produce the crop milk that both parents feed to their nestlings. In the Northwest, the reliance upon berries, which contain little mineral but much protein and energy, means that band-tailed pigeons must seek a mineral supplement to their diet. The limited number of available mineral sites may be the scarcest resource necessary for reproduction, and as a consequence band-tailed pigeons home strongly to mineral sites.

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Appendix A. Statistical Tables

Table A1. *Analysis of covariance for rate of increase of juvenile band-tailed pigeons observed at three mineral sites in western Oregon, 1975–76.*

Source of variation	df	Sum of squares	Mean squares	F	Probability
Treatment	2	79.23	39.12	61.2	0.0
Error	30	19.16	0.64		
Total	32	97.39	97.39		

Table A2. *Analysis of variance of fledging date of juvenile band-tailed pigeons based on wings collected from hunters by a mail survey in western Oregon, 1974–76.*

Source of variation	df	Sum of squares	Mean square	F	Probability
Model	7	3449.2	492.7	0.58	0.77
Year	2	1492.4	746.2	0.88	0.42
Region	5	1956.8	391.4	0.46	0.80
Error	272	230,296.8	846.7		
Total	279	233,746.0			

NOTE: The mention of trade names does not constitute endorsement or recommendation for use by the Federal Government.